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Vol. 74, No. 2 April 1976

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Seattle, Washington

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Fishery Bulletin

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GROWTH AND REPRODUCTION OF THE SPOTTED PORPOISE, *STENELLA ATTENUATA*, IN THE OFFSHORE EASTERN TROPICAL PACIFIC

WILLIAM F. PERRIN, JAMES M. COE, AND JAMES R. ZWEIFEL[1]

ABSTRACT

This study is based on data from several thousand specimens of spotted porpoise, *Stenella attenuata*, incidentally killed in the purse seine fishery for yellowfin tuna, *Thunnus albacares*. Average length at birth is 82.5 cm. Gestation is 11.5 mo. Average length at 1 yr is 138 cm. Length-weight equations are given for fetuses and postnatal males and females. Age was estimated from dentinal layers in thin sections of teeth. A two-phase Laird-Gompertz growth model was fitted to the layer-length data. Direct calibration of the dentinal layers beyond the first year (two layers) was not possible, and three alternative hypotheses were considered: 1) two layers per year, until pulp cavity occluded, 2) two layers per year in first year, and one per year thereafter, and 3) two layers per year until puberty, and one per year thereafter. The second alternative is most probably the correct one, but reproductive parameters were estimated in terms of layers. Breeding is diffusely seasonal, with prolonged calving seasons in spring and fall and a pronounced low in winter. A third calving season may exist in the summer. Average age at attainment of sexual maturity of males is approximately 12 layers (average length about 195 cm and average weight about 75 kg). Females attain sexual maturity on the average at about 9 layers and 181 cm. Ovarian changes in adult females are described. Apparently postreproductive females were encountered in the samples. It is concluded that corpora albicantia of ovulation and pregnancy persist indefinitely in the ovaries. It was not possible to distinguish between the two types of corpora. Ovulation rate changes with age, from about four per layer in very young adult females, to about one per layer in older females. The average calving interval is 26 mo long and consists of 11.5 mo of pregnancy, 11.2 mo of lactation, and 3.3 mo of resting and/or estrus. About 9.6% of lactating females are also pregnant. Pregnancy rate decreases with age, from about 0.6 per year at 8 to 10 layers, to about 0.3 at 16 layers. The overall sample contained 44.9% males and 55.1% females. Sex ratio changes with age, from near parity at birth, indicating higher mortality rates for males. Gross annual production of calves, based on age and sex structures of the sample and the estimated pregnancy rate, is 14.4% of the population per year. No evidence was found of age or sex segregation in schooling. The estimated parameters differ in a consistent way from those estimated for a population of *Stenella attenuata* in the western Pacific, possibly reflecting the exploitation in the eastern Pacific.

Porpoises of the genera *Stenella* and *Delphinus* are killed incidentally in the tuna seine fishery in the eastern tropical Pacific (Perrin 1969, 1970a; National Oceanic and Atmospheric Administration[2]). Since 1968, the National Marine Fisheries Service (NMFS) has conducted a program of research into the population biology of the major porpoise species to assess the impact of this fishing mortality on the porpoise stocks. The purpose of this paper is to describe the life history of the spotted porpoise, *Stenella attenuata* (Gray),[3] the animal most frequently killed in the fishery.

Little information on life history of the spotted porpoise has been available until very recently. Harrison et al. (1972) examined the gonads of 6 specimens from Japan (5 males and 1 female) and 45 specimens of *S. attenuata* from the eastern tropical Pacific (19 males and 26 females), but did not separate their results and conclusions from

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[2]National Oceanic and Atmospheric Administration. 1972. Report of the NOAA Tuna-Porpoise Review Committee, September 8, 1972. Unpubl. rep. U.S. Dep. Commer., Wash., D.C., 63 p.

[3]The taxonomy of the spotted porpoise has long been confused. Recent morphological studies (Perrin in press) have shown that the spotted porpoise in the tuna fishery is conspecific with the spotted porpoise occurring around Hawaii. The name *S. attenuata* (Gray 1846, holotype from unknown locality) applied by True (1903) to the Hawaiian form is used here for the eastern Pacific form, taking priority over *S. graffmani* (Lönnberg 1934). This usage is strictly provisional, pending the completion of current taxonomic studies, when a different name, such as *S. dubia* (G. Cuvier 1812) or *S. frontalis* (G. Cuvier 1829) may take priority.

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those for *S. longirostris*. Preliminary unpublished results of our studies indicate that these two species are probably disparate in such growth parameters as length at birth, length at maturity, and asymptotic length. Harrison et al. (1972) stated that lengths of the fetuses examined indicate that parturition occurs both in the spring and in the autumn. They described in detail the gross and microscopic histological appearances of several pairs of ovaries. A maximum of nine corpora albicantia were encountered. They concluded that if all the corpora albicantia in ovaries of specimens of this species do not represent past pregnancies, either the fertility is very low or the corpora are not permanent.

Nishiwaki et al. (1965) published length-frequency distributions of 34 fetuses (up to 106 cm long) and 194 postnatal animals (104 to 208 cm) from a school driven ashore in Japan. They estimated that gestation lasts 1 yr, length at birth is about 105 cm, juveniles reach 150 cm in 6 mo, and adult size (180 cm for females and 190 cm for males) is reached in 1 yr. They concluded that there are two seasons for mating and parturition, in the spring and in the autumn, and that there are fewer males than females among adults. Ontogenetic changes in coloration, external proportions, organ weights, the skeleton, parasite load, and feeding habits have been described (Perrin 1970b, in press; Perrin and Roberts 1972; Dailey and Perrin 1973; Perrin et al. 1973).

Kasuya et al. (1974) recently published results of a study of several hundred specimens caught in the Japanese fishery for *S. attenuata*. Their results are discussed and compared with ours in the body of this paper.

METHODS AND MATERIALS

Observer Program

Beginning in 1968, NMFS placed observers aboard U.S. tuna seiners to collect information on the incidental take of cetaceans in the eastern tropical Pacific. Observers were placed on 1 cruise in 1968, 5 in 1971, 12 in 1972, and 22 in 1973. Most of the cruises were 30 to 60 days long. In addition, biological data were collected during chartered cruises of commercial seiners: one in 1971, one in 1972, and two in 1973.

The data collecting had to be carried out in such a way as to not interfere with the fishing operation. Hence, the amount of information collected on the animals killed in a net set varied widely, depending on the amount of time that was available before the next set was made. Following is the hierarchy of types of data that were collected (sample sizes were largest for the first and smallest for the last):

Animals killed were:

1. Counted (estimates were made in cases where counts were not possible), usually on the deck or in the net,
2. Identified to species (and race when possible),
3. (*S. attenuata* only) identified to developmental color pattern phase (Perrin 1970b), and sexed,
4. Measured (to nearest centimeter with 2-m calipers), and
5. Dissected to collect information on reproductive condition (for females, mammaries were examined and reproductive tract collected; for males, the right testis was collected) and age (a section of the left lower jaw at midlength was collected). The gonadal material and jaw sections were preserved in 10% Formalin.[4] Small fetuses ($\leq$ 30 cm) were preserved in the uterus. Larger fetuses were removed from the uterus and frozen.

For each specimen that was at least measured (step 4 above), a field serial number was assigned, and a specimen data sheet was filled out. Data for specimens that were not at least measured were collected on a running tally.

The Study Area

One of us has described the distribution of *S. attenuata* in the eastern tropical Pacific (Perrin 1975). The known occurrence of mixed aggregations of cetaceans and tuna is strongly correlated with certain oceanographic conditions peculiar to that region. The porpoise-tuna association is known only in the eastern tropical portion of the Pacific. That area, which has been called the North Pacific Equatorial water mass (Seckel 1972), has an unusual oxygen-salinity-temperature structure. The reason for this is not

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

fully understood but certainly has to do with the latitude of the area, its position relative to the rest of the Pacific and to the American continents, and the shapes of the adjacent land masses. These factors interact with general global oceanic and atmospheric circulation to produce a water mass with relatively high surface temperature, low surface salinity, a strongly developed, shallow thermocline (usually within 100 m of the surface), and a pronounced, thick oxygen minimum layer just below the thermocline. The effect is to create a very extensive but shallow warm habitat with a sharp oxythermal floor. To the west, these conditions tail off along a divergence centered on lat. 10°N (Wyrtki 1964). The conditions must be causally interrelated, but one of the more striking correlations with the occurence of the mixed-species aggregation is in the thickness of the oxygen minimum layer (Figure 1).

The occurrence of the aggregation is not tightly correlated with the geographic distributions of the major prey species of the participating predators. Major shared prey items are the ommastrephid squid *Dosidicus gigas*, an unidentified ommastrephid (probably *Symplectoteuthis* sp.), a scombrid fish *Auxis* sp. (*A. thazard* or *A. rochei*), and the exocoetid fish *Oxyporhamphus micropterus* (Perrin et al. 1973). *Dosidicus gigas* is primarily equatorial but migrates sporadically as far as California and southern Chile, far beyond the limits of the distribution of the mixed-species aggregation (Clarke 1966; Young 1972). Species of *Symplectoteuthis* occur widely in the tropical Pacific and Indian oceans (Clarke 1966). *Auxis thazard* occurs in "tropical and subtropical waters of the Indo-Pacific and Atlantic oceans," and *A. rochei* in "tropical and subtropical waters of the Indo-Pacific and Atlantic oceans, including the Mediterranean Sea" (Richards and Klawe 1972). The genus *Oxyporhamphus* is also pantropical (Bruun 1935). At least some of the several myctophid fishes in the aggregate apparently are a mainstay of the diet of the spinner porpoise in mixed schools (Perrin et al. 1973) and are not restricted to the tropics but occur also in temperate waters of the eastern Pacific (Moser and Ahlstrom 1970) and elsewhere. These facts, combined with the pantropical distributions of the cetaceans, tunas, and birds, suggest that the multispecies aggregation does not have its roots in the distribution of the component species or their prey but rather in the peculiarities of the physical oceanography of the region.

The Sample

In 1971 and early 1972, when more specimens were decked than could be processed in the time available (the limit per net set was usually about 35 to 40 specimens), adult females were selected for measuring and dissection. The intention was to insure that sample sizes would be large enough to allow estimation of pregnancy rate with adequate precision. The information on age structure of the catch for that period is limited to the coloration phase data. The observer program subsequently expanded, and beginning in October 1972 no selection was practiced in determining which animals were to be dissected; the first 35 to 40 specimens of both sexes and all ages that came to hand were set aside for measuring and dissection and the remainder discarded. The length data for 1968 and for October 1972-December 1973 are presumably cross-sectional with respect to the kill.

The sample of animals at least measured included 3,504 postnatal animals and associated fetuses from known localities and 23 from imprecisely known localities (Figure 2). Coloration phase and sex data were collected for another 6,150 specimens. In addition, some data were available for 45 other specimens collected by other research agencies, museums, and private individuals. Because of the seasonal nature of the tuna fishery, the sample is heavily biased toward the early months of the year, with minimal coverage of the latter part of the year and practically no specimens from the summer months (Table 1).

Two races of *S. attenuata* exist in the eastern tropical Pacific — a large coastal form and a small offshore form (Perrin 1975, in press). This paper deals only with the offshore form. The estimates of life history parameters cannot be assumed to apply also to the coastal form.

TABLE 1.—Samples of postnatal spotted porpoise by month for all years.

Month	Males	Females	Total
January	748	443	1,191
February	263	209	472
March	298	147	445
April	216	155	371
May	181	97	278
June	69	58	127
July	1	0	1
August	6	5	11
September	0	0	0
October	222	158	380
November	110	87	197
December	30	24	54
Total	2,144	1,383	3,527

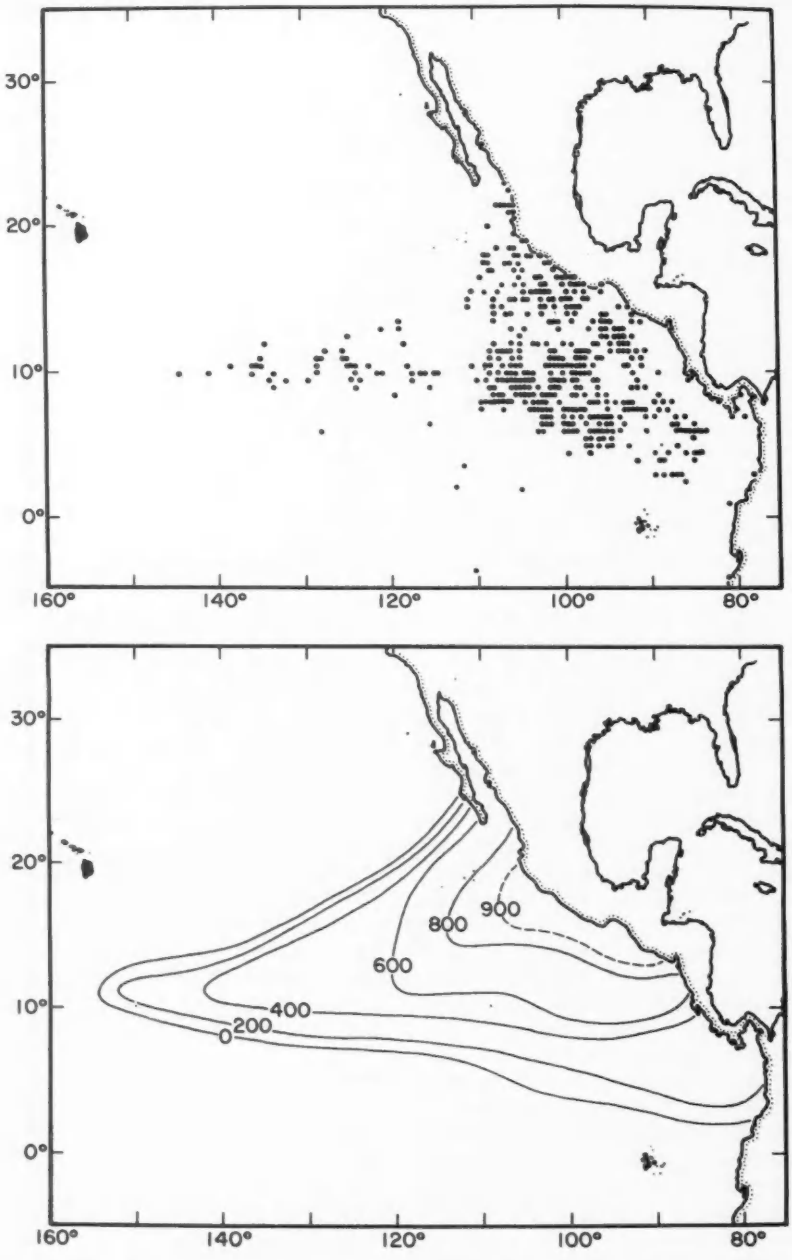

FIGURE 1.—Comparison of the known occurrence of spotted porpoise in the eastern Pacific (above) with average thickness of the subsurface layer of water (contours in meters) in which the dissolved oxygen is less than 0.25 ml/liter (below, after Knauss 1963). The entire layer lies above 1,000 m.

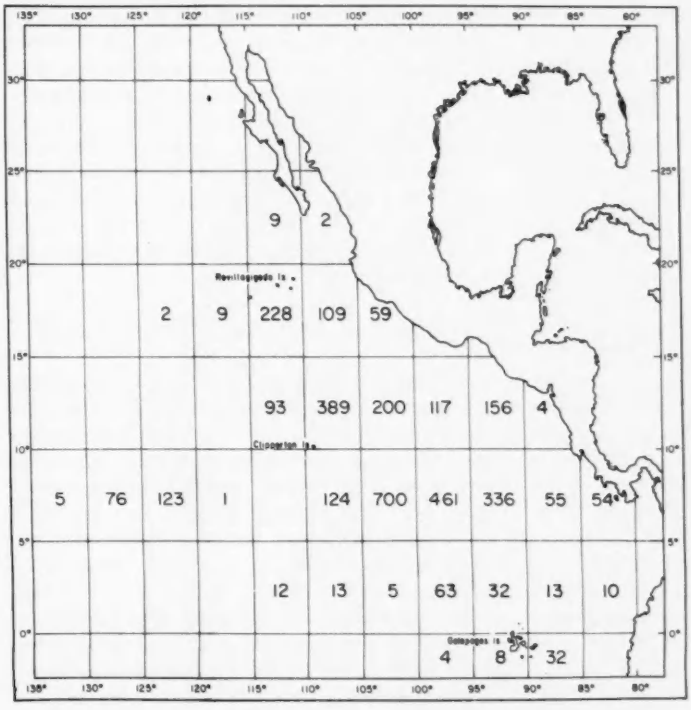

FIGURE 2.—Samples of spotted porpoise used in life history studies by 5° square. Does not include specimens that were not at least measured.

Because the field program is a continuing one, the sample sizes for the various analyses were different and depended on how much material was available at the time each analysis commenced. Restrictions on sample size are set out in the text below.

Laboratory Procedures

Fetuses were measured with dial calipers or with calipers mounted on a 1-m stick. Postnatal animals were weighed to the nearest pound on platform scales. Fetuses were weighed to the nearest gram on a triple beam balance. Testes were weighed to the nearest gram on a platform balance. A 1-cm^3 cube from the center of each testis[5] and a similarly sized sample of the epididymis from midlength of the testis were sectioned and stained with hematoxylin and eosin. The mounted sections were subsequently examined under a compound microscope.

Ovaries were weighed to the nearest 0.1 g on a platform balance. They were then cut into transverse sections approximately 1 mm thick with a scalpel and the sections examined under a dissecting microscope. The corpora albicantia in each ovary were scored to eight categories based on size, color, vascularization, and gross appearance (categories described below). If a corpus luteum was present, it was measured with dial calipers to the nearest millimeter in its three largest dimensions. The diameter of the largest follicle was measured to the nearest 0.1 mm.

Age was estimated for 442 animals by examination of dentinal layers in the teeth. Three or four teeth were extracted from the lower right tooth row at approximately midlength and mounted on wooden blocks in dental wax or plastic resin. A longitudinal section 0.012 inch (0.31 mm) thick was cut from each tooth with a diamond saw. The sections were cleared for several days in a 1:1 mixture of glycerine and 95% ethanol, mounted under cover slips in balsam, and examined with transmitted light under a

[5]Some early samples were taken near the dorsal surface of the testis. Tubule diameter in these was subsequently found not to differ relative to length, weight, and age of the animal from that in those taken at the center of the testis, and the lots were therefore combined for analysis.

compound microscope at approximately 30 diameters. One postnatal layer was considered to consist of an opaque subunit and a translucent subunit (Figure 3). The layers in most of the teeth examined were not as well-defined or as regular in thickness as those illustrated by Kasuya (1972) for *Stenella coeruleoalba* or by Klevezal' and Kleinenberg (1969) for *Delphinus delphis*. Teeth from 39 of the 442 animals were completely unscorable, being heavily worn or showing no discrete layers in the sections examined. All the teeth were scored several times, over a period of several months, without referring to specimen numbers or to values obtained previously, until the scorer felt confident of the results. The values used in the analyses are those obtained in the final round of scoring. The teeth were scored to the nearest postnatal layer when possible, or a range, e.g., "8 to 10 layers," was estimated. Average accuracy is estimated at ±1 layer for teeth with 5 layers or less and ±2 layers for teeth with 5 to 12 layers. Convoluted secondary dentine was present in most of the teeth with more than 12 layers, making counts very difficult and of dubious reliability. We feel that the counts for many of these teeth are probably underestimates. Teeth in which the pulp cavity was entirely closed in all sections examined were scored as "occluded."

The NORMSEP computer program was used to define modes in the length-frequency distributions for fetuses. The program was written by Hasselblad (1966) and modified by Patrick K. Tomlinson, Inter-American Tropical Tuna Commission. The program separates the mixture of normal length distribution into its components, assuming that the lengths of individuals within age groups are normally distributed and that an unbiased sample of the length distribution was obtained.

GROWTH

Length at Birth

Average length at birth of 82.5 cm was obtained from a linear regression line based on 3-cm groupings of fetuses and neonatals (Figure 4). The largest fetus of the 461 examined was 904 mm long. The smallest neonatal animal was 780 mm long. Eighty-six calves and fetuses between 73 and 94 cm were measured in random samples. Assumptions inherent in the method used to arrive at this estimate are that pregnant females and calves are 1) equally vulnerable to capture in the purse seine, 2) equally likely to die once captured, and 3) equally represented in the sample of dead animals measured. For example, if neonates were less likely to be included in the samples than were pregnant females, average length at birth would be overestimated. Other potential sources of error are differential rates of prenatal and postnatal natural mortality and premature births caused by stresses imposed by pursuit and by capture in the purse seine.

Gestation Period and Fetal Growth

The most commonly used method for estimating the gestation time of cetaceans is that of Huggett and Widdas (1951). They showed that for a variety of mammals of widely different orders, a plot of the cube root of fetal weight on age is linear except during the first part of pregnancy, when growth is exponential. Their model can be expressed in the general formula $W^{1/3} = a(t - t_0)$, where W = weight, t = age, a = the "*Specific Fetal Growth Velocity*," and t_0 = "the intercept where the linear part of the plot, if produced backwards, cuts the time axis." Laws (1959) applied the method of Huggett and Widdas to fetal length/time data for three odontocetes (*Physeter catodon*, *Delphinapterus leucas*, and *Phocoena phocoena*) and obtained estimates of gestation periods (15, 14, and 11 mo, respectively). He assumed that weight is proportional to the cube of length and used the form $L = a(t_g - t_0)$, where L = length. This assumption is not entirely correct (see length-weight results below), but is a close enough approximation of the real relationship between length and weight to allow its use in estimating gestation period. Laws' estimates corresponded closely with other estimates obtained by more direct methods. Laws' version of Huggett and Widdas' method is used here.

A gestation period of 11.5 mo was obtained from an analysis based on 281 fetal and postpartum specimens collected in January, February, March, April, May, and October 1972 (Figure 5). The January-May samples comprised all of the fetuses of all of the females examined. The postpartum samples in these months were not random and are therefore not included. The October samples were random over all age-classes in the catch; therefore, all specimens less than 160 cm long, approximately the length at onset of puberty (Harrison et al. 1972), are included in the plot. Obvious modes are present in the length distributions (seasonal-

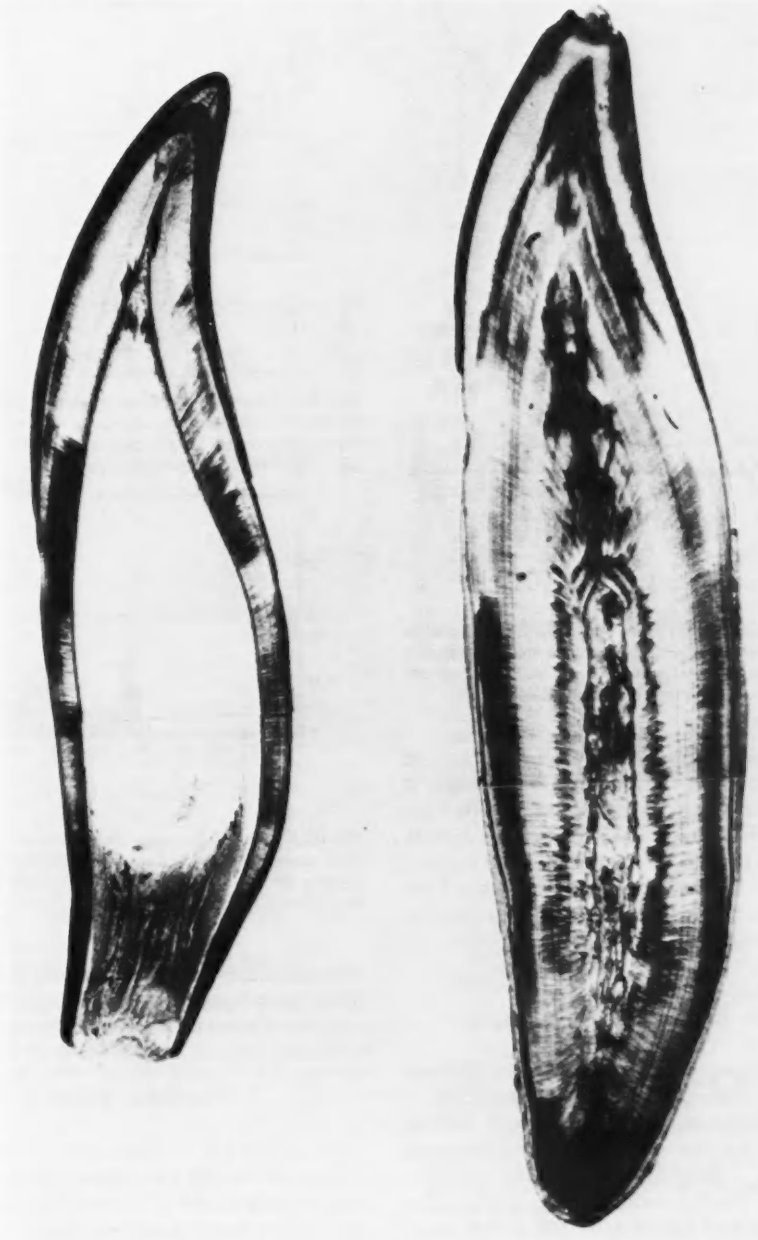

FIGURE 3.—Longitudinal thin sections of teeth from two specimens of *Stenella attenuata* from the offshore eastern tropical Pacific. (Left) field number CV300 male, 144 cm, with two postnatal dentinal layers; (right) number LR55 female, 191 cm, with 13 layers.

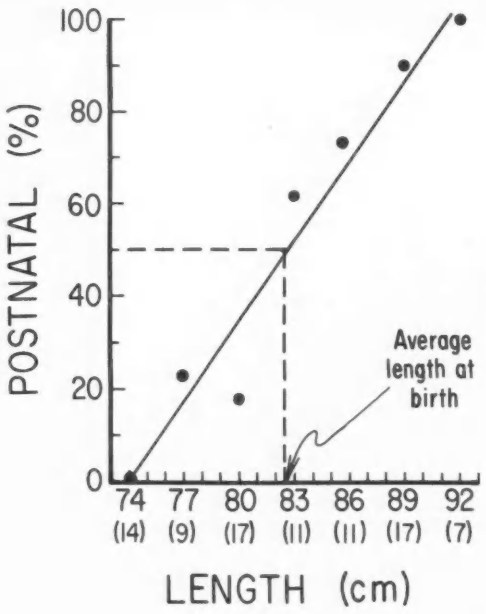

FIGURE 4.—Linear regression analysis of percent postnatality on body length for 86 fetuses and calves of *Stenella attenuata* from the offshore eastern Pacific grouped in 3-cm intervals. Sample size for each 3-cm interval in parentheses.

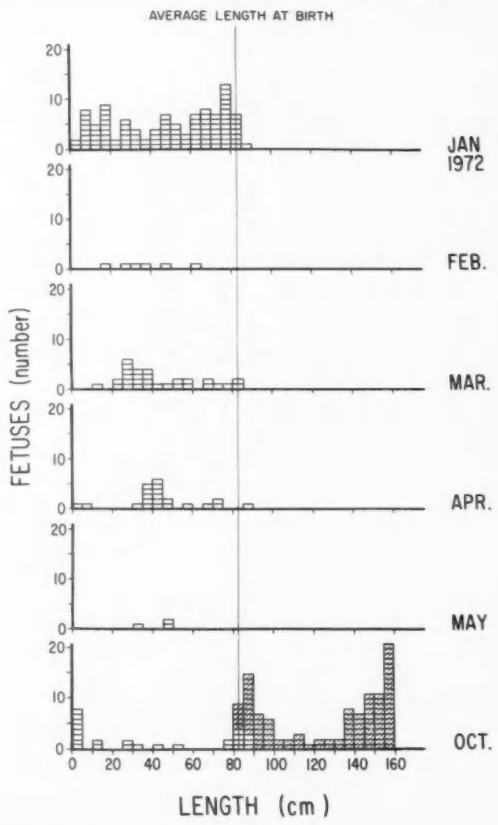

FIGURE 5.—Length-frequency distributions by month for 281 fetal (open) and young (hatched) postnatal specimens of *Stenella attenuata* captured by tuna seiners in the offshore eastern tropical Pacific in 1972.

ity is discussed below). Apparent progression of the smaller mode in the January 1972 sample is consistent with a gestation period of roughly 1 yr. Sample sizes for the other apparent modes are not large enough for similar analysis. Linear regression analysis of the modal lengths plotted on month (Figure 6) yields an estimate of the slope to use in Laws' equation:

$$L = 8.283\ (t - t_0), \text{ or}$$
$$\text{length at birth} = 8.283\ (t_g - t_0)$$

with $(t_g - t_0)$ (using months of 30.4 days) = 9.96 mo or 303 days, where t_g = total gestation period.

Laws (1959) proposed that t_0 for length data is slightly less than for weight data and assumed $t_{0_{Ln}} = 0.9\ t_{0_{wt}}$. Roughly interpolating between Huggett and Widdas' values for $t_{0_{wt}}/t_g$ of 0.1 for $t_g > 400$ days and 0.2 for $t_g = 100$ to 400 days (using provisional $t_g \cong 330$ days to enter the iteration) (Figure 7) and applying Laws' correction, $t_{0_{Ln}}$ of $\cong 0.135\ t_g$ is obtained. This value yields an estimate of gestation time of 11.5 mo (349 days). The estimate of t_0 (47 days) is crude, but the true value probably lies between $0.12\ t_g$ and $0.15\ t_g$. We therefore estimate the gestation period to be 11.5 ± 0.2 mo (interval between estimates using $t_0 = 0.12\ t_g$ and $0.15\ t_g$), or 11.3 to 11.7 mo.

Postnatal Growth

The same cohort used for analysis of fetal growth can be followed through the samples until approximate length of 125 cm (Figure 8) at the age of approximately 8.5 mo. In order to optimize resolution, 4-cm intervals were used, and the samples for April, May, and June were combined. Modes were estimated with NORMSEP.

A linear regression line through the modal lengths yields the postnatal growth equation

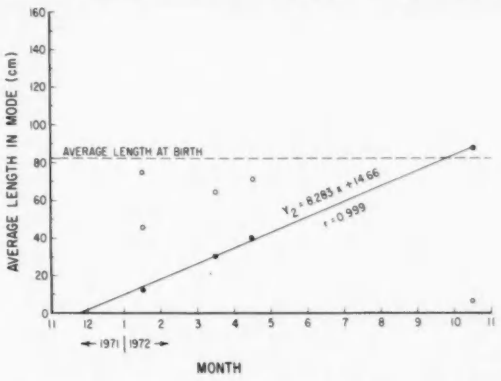

FIGURE 6.—Linear regression analysis of modal lengths of fetal and neonatal specimens of *Stenella attenuata* (from Figure 4). Open circles are modes not included in the analysis. Modal lengths defined with computer program NORMSEP (see Materials and Methods).

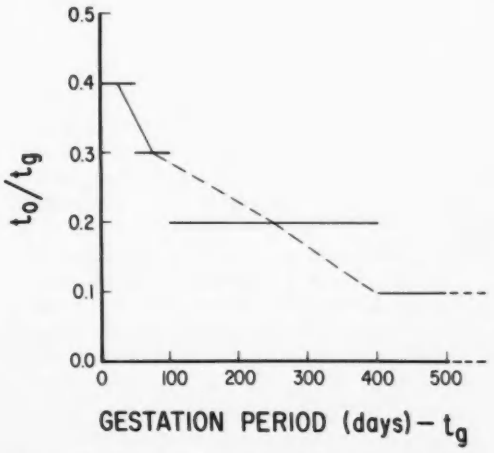

FIGURE 7.—Ratio t_0/t_g interpolated between empirical estimates of Huggett and Widdas (1951)—"...for gestation times up to 50 days $t_0 \triangleq 0.4 \times$ (gestation time), from 50-100 days $t_0 \triangleq 0.3 \times$ (gestation time), from 100-400 days $t_0 \triangleq 0.2 \times$ (gestation time), over 400 days $t_0 \triangleq 0.1 \times$ (gestation time)."

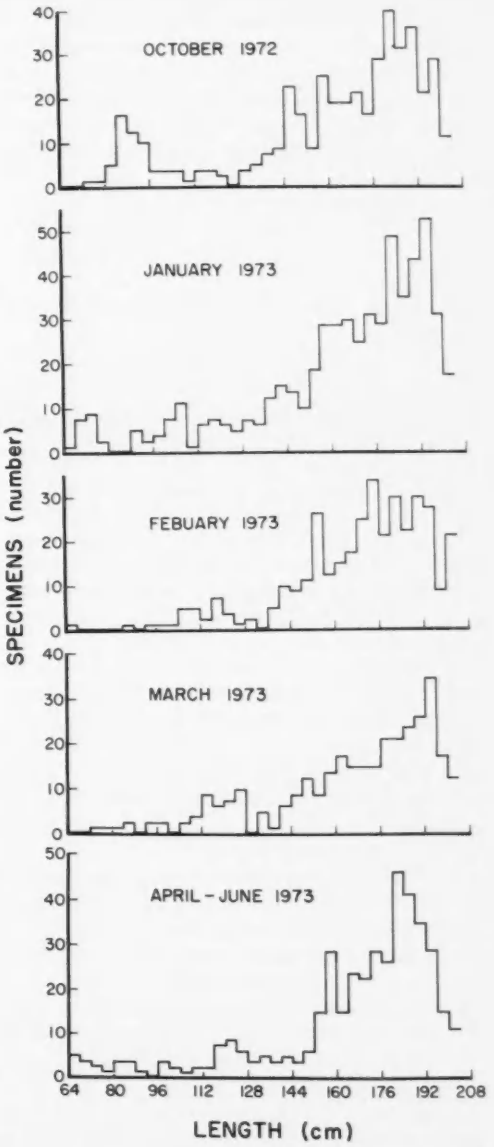

FIGURE 8.—Length frequencies of fetuses and postnatal specimens of *Stenella attenuata* between 64 and 204 cm long, of both sexes, by month.

$$L = 82.5 + 5.42\,t,$$

where L = length in centimeters
t = postnatal age in months.

Analysis Based on Analogy with Other Cetaceans

Fetal growth in length of cetaceans, except for an initial slow phase (t_0), is nearly linear. Postnatal growth during at least a period equivalent in length to the gestation period is also nearly linear, but at a lower rate. The difference between the

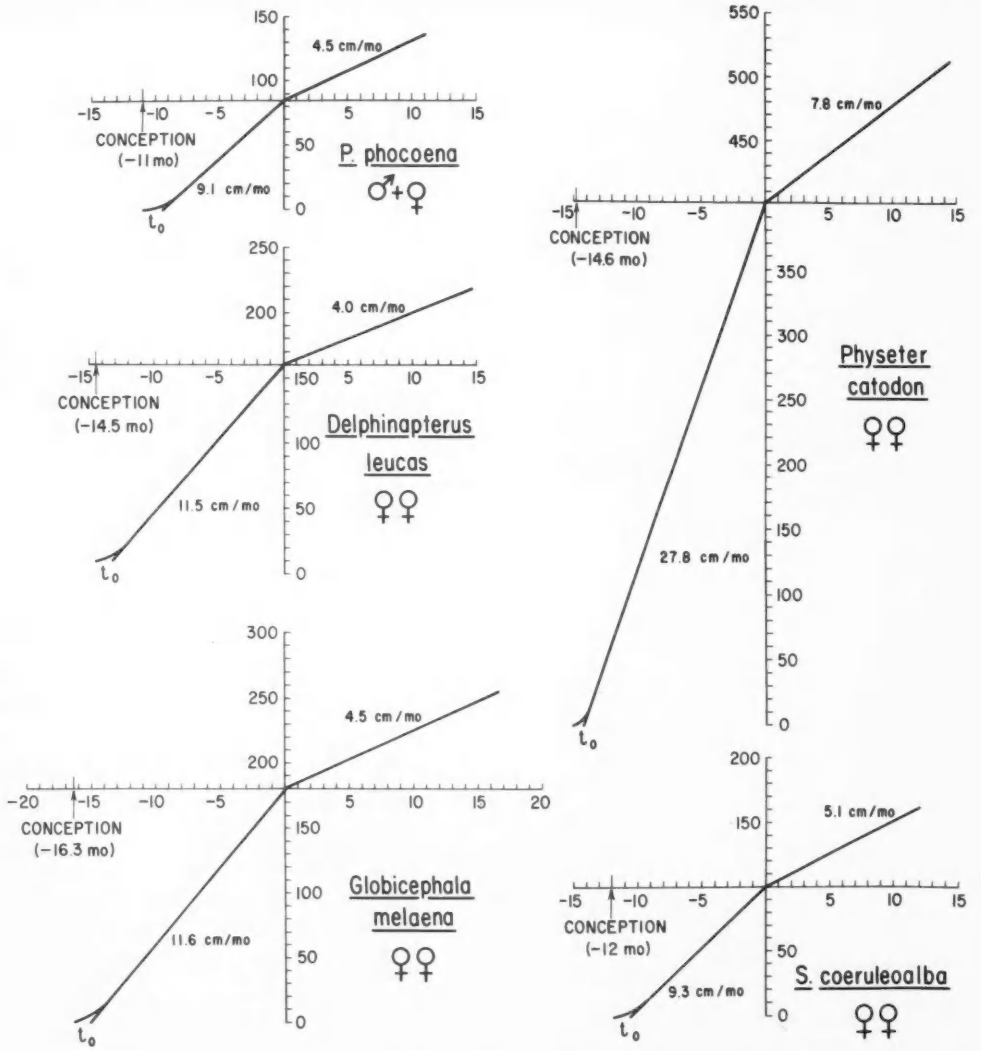

FIGURE 9.—Fetal growth and average postnatal growth during a period equal to the gestation period in five odontocete cetaceans: *Phocoena phocoena* (gestation period and postnatal growth from Møhl-Hansen 1954; t_0 from Laws 1959; length at birth from Fisher and Harrison 1970); *Delphinapterus leucas* (from Brodie 1971); *Globicephala melaena* (from Sergeant 1962); *Physeter catodon* (from Best 1968, 1970); and *Stenella coeruleoalba* (from Kasuya 1972).

fetal rate and the average rate during a postnatal period equal to the gestation period differs among the five odontocete species for which sufficient data exist (Figure 9) and is correlated with length at birth (Figure 10). The least-squares line for log of the difference between fetal and postnatal growth rates (Y) on log of length at birth (X) yields $Y = -1.33 + 0.997X$, from which a predicted Y of 3.75 cm/mo is estimated for *S. attenuata* and an average growth rate in the first year of 4.66 cm/mo is estimated. This average rate is close to those for the other three delphinids (5.1 for *S. coeruleoalba*,

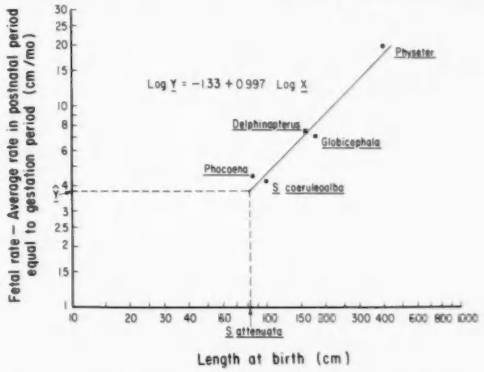

FIGURE 10.—Relationship of difference between fetal growth rate during linear phase and average growth rate during postnatal period equal to gestation period to length at birth in five odontocete cetaceans. Line is linear regression line of log difference on log length. Data from Figure 11. $\hat{Y}$ is predicted difference for *Stenella attenuata* from the offshore eastern tropical Pacific.

4.5 for *Globicephala*, and 4.5 for *P. phocoena*)[6]; and yields a predicted length at 1 yr of 138 cm.

Length Relative to Tooth Layers

Total length was plotted on number of postnatal layers for 115 males and 306 females (Figure 11). The teeth of five males and three females had completely filled pulp cavities. These are included in the plots in a separate category "occluded."

The plots of means for 2-layer intervals (the points in Figure 12; the curves were fitted as explained below) very closely resemble the growth curve obtained by Sergeant (1962) for *Globicephala*. Asymptotic length (L_∞) for females is approximately 190 cm and for males approximately 200 cm. There appears to be a secondary surge in growth at about 6 layers. With the restriction that the curves must pass through birth length of 82.5 cm and asymptotic lengths of 190 and 200 cm, it is not possible to fit any continuous equation to the data satisfactorily. Continuous curves that fit well at the upper and lower ranges of layer count seriously underestimate length at 5 to 7 layers. Kasuya (1972) also encountered difficulty in attempting to fit a continuous model to growth of a delphinid, *S. coeruleoalba*. Good fits can be obtained, however, by assuming a dynamic growth function. A two-phase version of Laird's (1969) growth model was fitted to the 2-cm means for all males and females, using an iterative least-squares method. The occluded specimens were assigned to the 16+ interval.

Laird's model is

$$L(t) = L_0 \exp\left\{\frac{a}{\alpha}\left[1 - \exp(-\alpha t)\right]\right\},$$

where

$L(t)$ = length at time t
L_0 = length at birth (82.5 cm in this case)
t = time (layers in this case)
a = specific rate of exponential growth
α = rate of decay of exponential growth.

This model assumes that an organism's growth pattern is determined at conception. The fitted parameters a and α express the premise that "growth is fundamentally exponential (implied by the normal binary fission of cells), and it also undergoes exponential retardation by some as yet unknown physiological mechanism" (Laird 1969).

In the two-phase approach, separate equations were simultaneously fitted to the upper and lower range of means. The assumptions were made that juvenile growth is the same for males and females (supported by the data) and that the growth discontinuity comes at about the same age for males and females. The only fixed point was 82.5 cm at 0 layers (birth). The convergence point (inflection in the growth curve) was allowed to float to the position that gave the best fit, with males and females considered jointly for lesser ages. The equations converged at 5.59 layers (rounded off to 6 below) at which predicted length is 159.9 cm. The fit is excellent for females (Figures 11, 12). Asymptotic length is 190 cm at predicted age of 18 layers. Average length of adult females (those with ovarian scars) is 187.3 cm, based on a sample of 555 (Perrin 1975). The largest female of 2,138 measured was 220 cm long. The equation for juvenile growth to less than 6 layers is

$$L = 82.5 \exp\left\{\frac{0.4817}{0.7172}\left[1 - \exp(-0.7172t)\right]\right\},$$

where L = length, in centimeters
t = age in layers.

[6]Fisher and Harrison (1970) stated that their data suggest that *Phocoena* in Canadian waters grows approximately 30 cm during the first year of life, or at an average rate of about 2.5 cm/mo, as opposed to the 4.5 cm/mo hypothesized by Møhl-Hansen (1954). However, they also suggested, and their figure 2 showed, an average rate of at least 5 cm/mo during the first 4 mo. It seems unlikely that the rate would drop to an average of ~ 1.25 cm/mo in the remaining 8 mo of the first year.

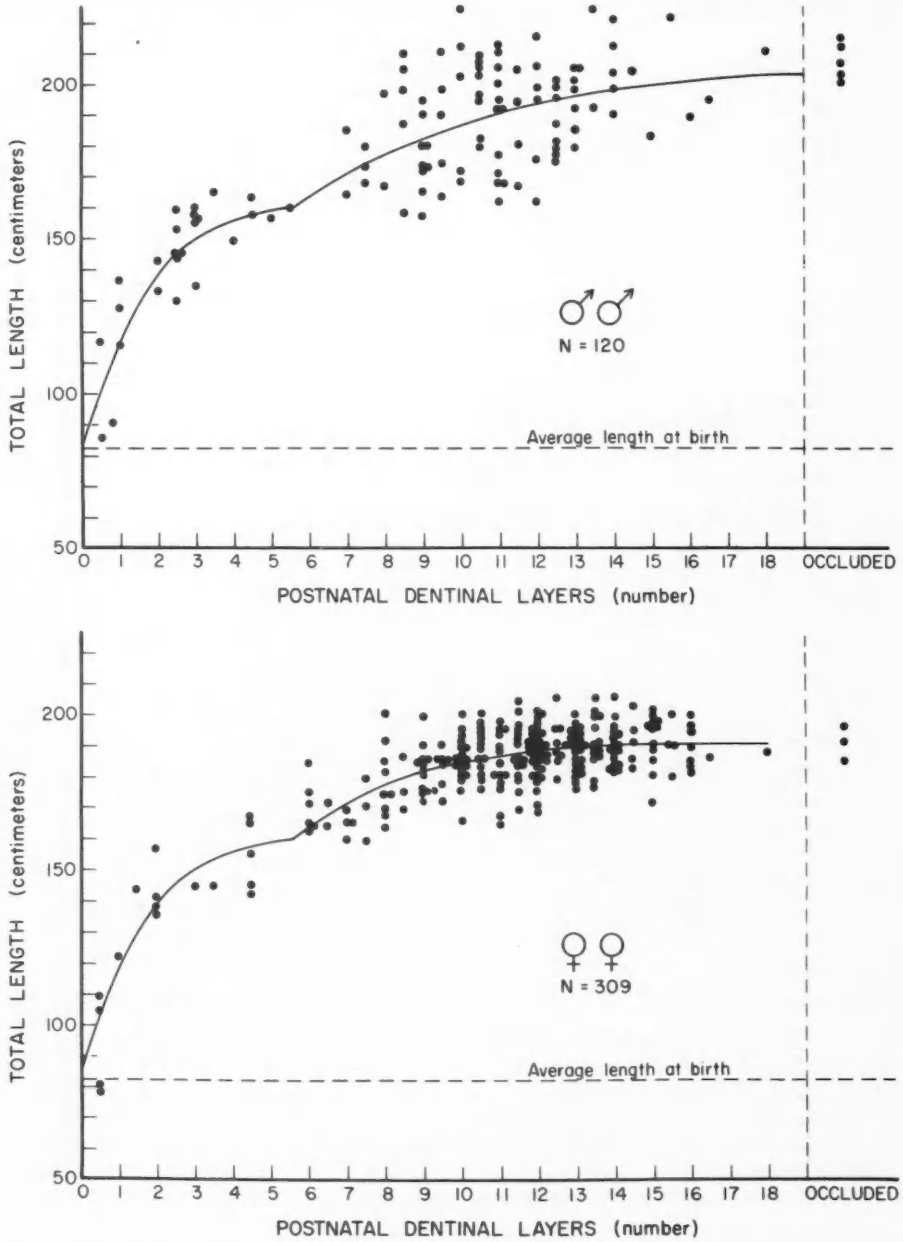

FIGURE 11.—Scatterplots of body length on number of postnatal dentinal layers from males (top) and females (bottom) of *Stenella attenuata* from the offshore eastern Pacific. Lines are fit to the growth model (see text).

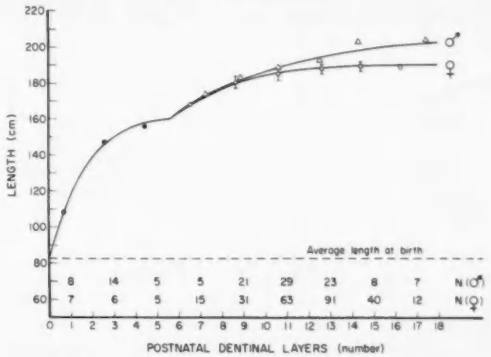

FIGURE 12.—Fit of the double Laird growth model (see text) to 2-cm mean values of body length on number of postnatal dentinal layers for males and females of *Stenella attenuata* from the offshore eastern Pacific. For samples greater than 30, ± standard errors indicated as vertical line.

For females with 6 or more layers, the growth equation is

$$L = 159 \exp\left\{\frac{0.0657}{0.3707}\left[1 - \exp\left(-0.3707(t - 5.588)\right)\right]\right\}.$$

In this case, both the growth rate and the rate of decay of growth are sharply lower than for juveniles.

The fit for males is not as good (Figures 11, 12) as it is for females, probably due to greater variability and to inadequate sample sizes for the two oldest strata (the tooth-reading effort was concentrated on females because of their importance in population dynamics). Another possible explanation for the relatively poorer fit for males is that growth (real, or as inferred from tooth layers) in adult males is more complex than in adult females, and a model more complex than the Laird model is called for. Inferred asymptotic length is 206 cm, achieved at predicted age of 26 layers. Average length of adult males (defined as those having testes weighing 200 g or more) is 200.7 cm, based on a sample of 253 (Perrin 1975). The largest male of 1,083 measured was 226 cm long. The growth equation for males with 6 or more layers is

$$L = 159.5 \exp\left\{\frac{0.0524}{0.2032}\left[1 - \exp\left(-0.2032(t - 5.588)\right)\right]\right\}.$$

The secondary growth rate (α, 0.0524) is very slightly smaller than for females, but the rate of decay (α, 0.2032) is sharply smaller, reflecting the attainment of greater size in males. The equations rearranged and reduced for estimating age (in terms of layers) from length are

$$t(\text{M and F} < 160 \text{ cm}) = -1.394 \ln (7.531 - 1.48 \ln L)$$

$$t(\text{F} \geq 160 \text{ cm}) = 5.588 - 2.698 \ln (29.606 - 5.64 \ln L)$$

$$t(\text{M} \geq 160 \text{ cm}) = 5.588 - 4.921 \ln (20.669 - 3.878 \ln L).$$

Note: These equations should not be used to estimate age from length except for grouped samples of smaller animals (about 180 cm or less), for which growth rate is still large compared to individual variation in length.

The juvenile growth curve based on tooth layers can be calibrated for the first year by comparison with the growth curve derived from analysis of modal progression (above) and by deduction from what is known about juvenile growth of other odontocetes (the fetal-postnatal growth argument above). Estimated average length at 8 mo based on analysis of modal progression is 125.5 cm. The predicted number of layers at that length (Figure 12) is 1.53. If the average growth rate during the first year is assumed to be the same as the average during the first 8 mo, the predicted number of layers at 1 yr ($1.53 \cdot 12 \div 8$) is 2.3. This extrapolation, however, is a slight overestimate, because while growth during the first year in delphinids is approximately linear, there is some decay of rate. The predicted number of tooth layers (using Figure 12) at 138 cm, the above-predicted length at 1 yr based on camparison with other odontocetes, is 2.0. It seems safe to assume that about 2 layers are laid down during the first year of life.

Calibration of the remainder of the tooth-layer curve is more difficult. Kasuya et al. (1974) examined the innermost layer in teeth of *S. attenuata* and related type and thickness of layer to season of capture. They concluded that one layer (one transparent plus one opaque subunit) represents 1 yr of growth. We found no correlation between thickness of the innermost layer and season of capture. Almost all of the samples for which teeth were sectioned, however, were collected in the first few months of the year. Lacking such direct calibration, several alternative possibilities can be examined. The results, however,

must remain tentative and inconclusive until growth has been monitored directly in one or more captive or free-ranging, tagged individuals.

Some alternatives that can be considered are:

1. Two layers per year until the teeth are occluded.
2. Two layers in the first year and one per year thereafter until the teeth are occluded.
3. Two layers per year until puberty (about nine layers in males and seven in females; see section below on age at puberty), and one per year thereafter.

This list of alternatives can be extended to great length by making assumptions such as that layers are laid down at irregular intervals, males and females lay down layers at different rates, layers disappear with age, etc., but the above are probably the main possibilities that should be considered. All references below to age are in terms of layers, with the above alternative possibilities considered or implied. None of the alternatives can be eliminated with certainty. One tooth layer deposited per year has been inferred for the western Pacific population of *S. attenuata* by Kasuya et al. (1974). One layer per year has also been suggested for other closely related delphinids, including *S. coeruleoalba* (Kasuya 1972) and *Tursiops truncatus* (Sergeant et al. 1973). Two tooth layers per year have been found in *Delphinapterus leucas* (Sergeant 1973), but this form is less closely related to *Stenella*. Thus, there is more support in the literature for the one-layer-per-year model (number 2 above) than for the others.

Length-Weight Relationships

Length-weight relationships were determined for 218 fetuses, 66 postnatal males, and 33 nonpregnant, postnatal females by using linear regressions of log weight on log length.

Fetuses

The fetuses ranged from 20 to 897 mm long and weighed from 2 to 7,588 g. Ten fetuses less than 20 mm long were not included. The regression equation is

$$\log W = 3.5532 + 2.501 \log L,$$

where W = weight in grams
L = length in millimeters.

In exponential form, the relationship is

$$W = 2.79 \times 10^{-4}\ L^{2.501}.$$

Females

The females ranged from 100 to 200 cm and weighed from 12.0 to 69.1 kg. The regression equation is

$$\log W = -4.1576 + 2.6120 \log L,$$

where W = weight in kilograms
L = length in centimeters, or in exponential form, $W = 6.95 \times 10^{-4}\ L^{2.612}$.

Males

The males ranged from 86 to 218 cm and weighed from 6.8 to 90.0 kg. The regression equation is

$$\log W = -4.7135 + 2.873 \log L,$$

where W = weight in kilograms
L = length in centimeters, or in exponential form, $W = 1.93 \times 10^{-5}\ L^{2.873}$.

The slopes of the regression equations are statistically different (t-test at $\alpha = 0.05$) for males and females. Males are lighter for their length at birth, and heavier for their length after about 135 cm has been attained.

Color Pattern

Perrin (1970b) has previously described the development of the color pattern of *S. attenuata* in the offshore eastern Pacific. The animal begins life unspotted, develops dark spots ventrally that later coalesce, as light spots develop dorsally. The ontogenetic continuum can be divided into five stages as defined below and as shown in Figures 13 and 14:

1. *Newborn stage.* Dark purplish-gray dorsal surfaces and lateral blazes, with white ventral surfaces and no spots; about 80 to 160 cm.
2. *Two-tone stage.* General two-tone pattern with dark-gray surfaces above, lighter gray lower surfaces, and a well-defined pattern in varying shades of gray about the head and flippers; no spots; about 95 to 175 cm.

The division between this and the previous category is somewhat subjective and arbitrary.

3. *Speckled stage.* Same as two-tone but with discrete, very dark-gray spots on the ventral surfaces; discrete light-gray spots on the upper, darker surfaces present on some animals but lacking on others; about 140 to 190 cm.

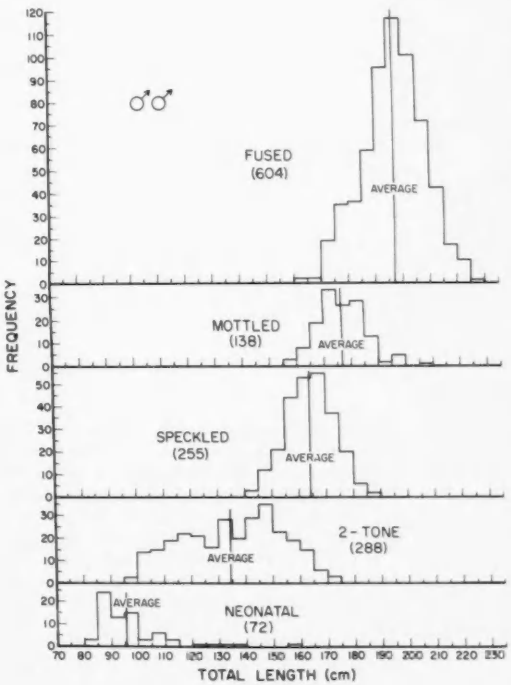

FIGURE 13.—Length-frequency distributions of males of *Stenella attenuata* from the offshore eastern Pacific, by color pattern phase.

4. *Mottled stage.* Ventral spots converging and overlapping in places, but patches of the lighter gray background still visible, yielding a mottled effect; discrete or merging light-gray spots present on the upper surfaces; about 155 to 210 cm.
5. *Fused stage.* Ventral spots completely convergent, to give the effect of a uniform, medium-gray to dark-gray surface; on close inspection, the individual overlapping spots still discernible; about 160 to 230 cm.

REPRODUCTION

Seasonality

Nishiwaki et al. (1965) suggested that *S. attenuata* in Japanese waters breeds in the spring and in the autumn. Harrison et al. (1972) stated that lengths of fetuses indicate that parturition in the eastern tropical Pacific (of *S. graffmani* = *S. attenuata*) also occurs both in the autumn and in the spring. The postnatal length-frequency data for large samples (Figures 15, 16; April 1968 and October 1972, for example) support the thesis of major reproductive seasons in spring and autumn but also suggest that there is a reproductive peak in summer as well. There is year-to-year variation in the timing of reproductive peaks, and there is some reproduction occurring throughout most of the year. It is difficult to define the reproductive seasons with precision because most of the sampling effort was in the early (January-April) and late (October-December) parts of the calendar year. The sampling intersected obvious calving seasons in April 1968, January 1972, October 1972, January 1973, and June 1973 (Figures 15, 16). Calving peaks were probably also present in some of the other sampling months, but the samples were too small to detect them or were biased in some fashion. A summary of predicted birth dates for 373 fetuses more than 15 cm long collected in 1971, 1972, and 1973, however, indicates that there may have been three calving peaks in each of the 3 yr (Figure 17). In each year there was a definite calving low in winter. The synchrony was diffuse, and some peaks were much sharper than others. The statistical evidence for three annual peaks in calving is weak, and when the data for all years are combined, all that can be said with certainty is that the calving season is prolonged, with a low point in winter and a tendency for high points in spring and fall.

The Male

Sexual development of the male was examined under three criteria: 1) weight of testes, 2) average diameter of seminiferous tubules, and 3) amount of sperm in the epididymis. Each of these was examined relative to total length, weight, and age (number of postnatal dentinal layers).

Weight of the testes (Figure 18) increases precipitously at body length of about 175 to 190 cm,

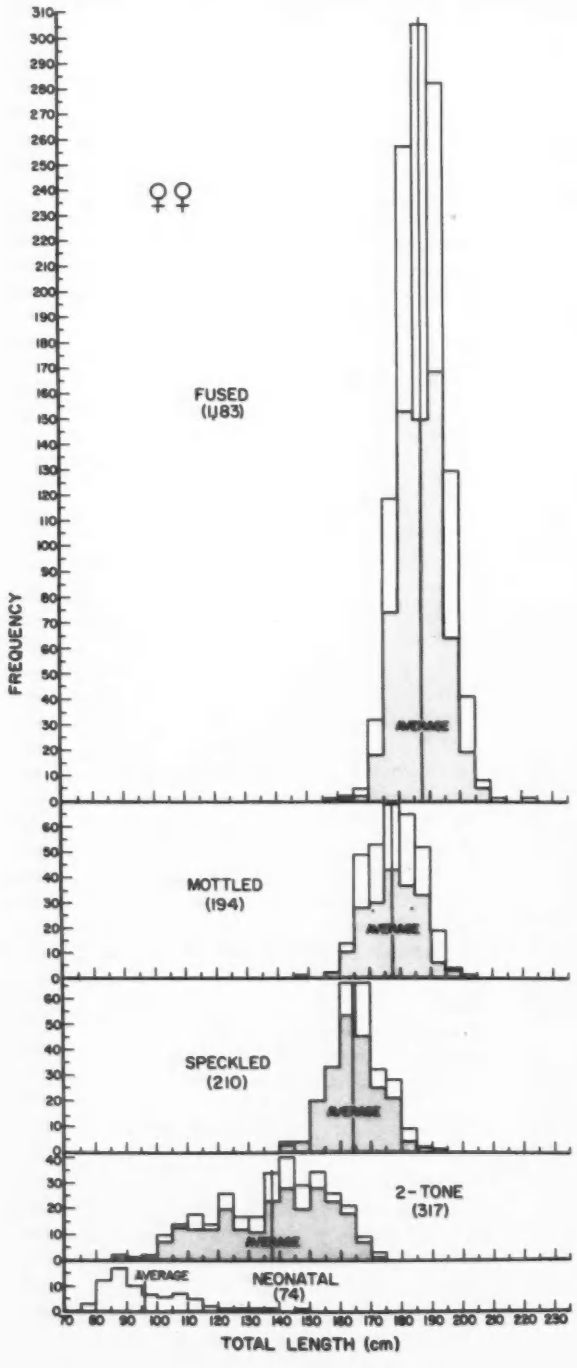

FIGURE 14.—Length-frequency distributions of females of *Stenella attenuata* from the offshore eastern Pacific, by color pattern phases. On cruises between January 1971 and October 1972, adult females (≥160 cm) were selected for measuring and dissection. Earlier and later samples were nonselective. Average lengths for neonatal, two-tone, and fused are based on all the samples (no length bias), and averages for speckled and mottled are based on the nonselective samples (shaded). The analyses of coloration transition are based on all the samples for neonatal-to-two-tone and on the nonselective samples for the remaining three transitions. Size of sample used for calculation of average is given in parentheses.

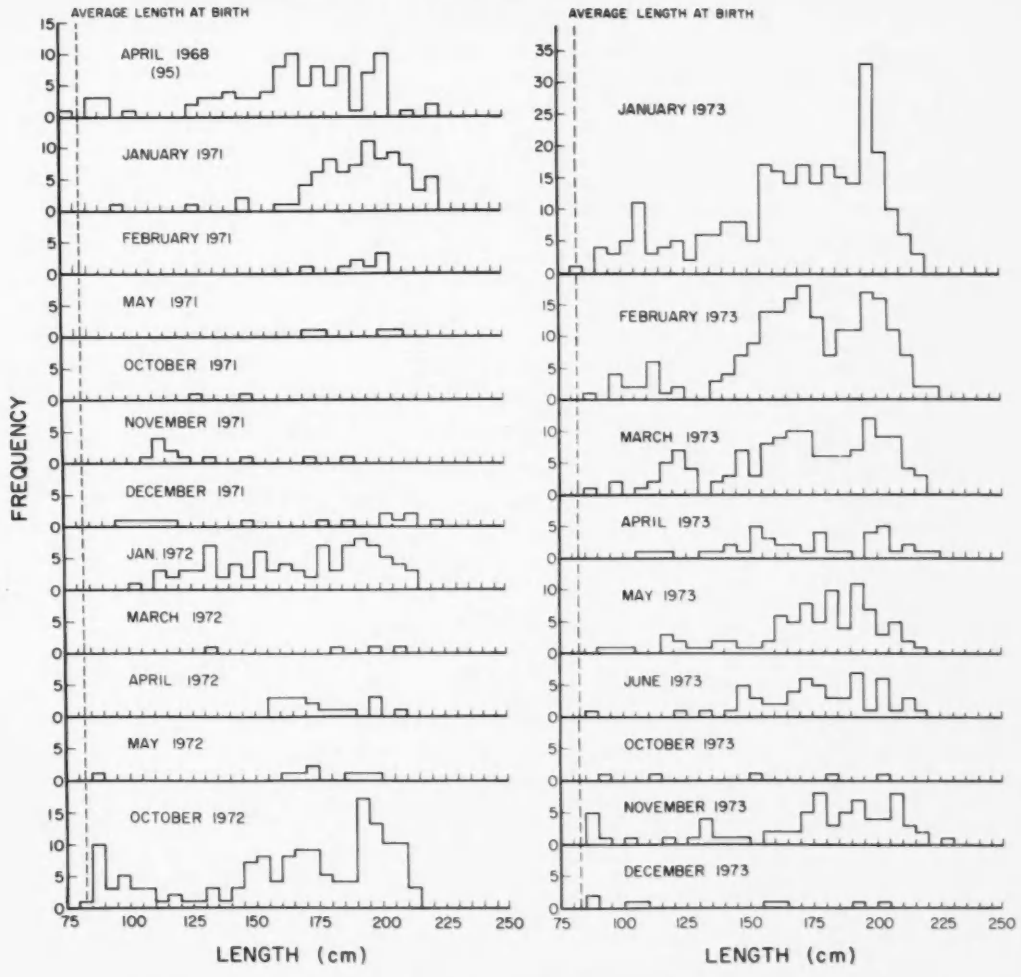

FIGURE 15.—Length-frequency distributions of postnatal male specimens of *Stenella attenuata*, 1968-73, by month.

but in animals larger than about 200 cm, there is little correlation with length. The largest testes encountered weighed 2,400 g and were possessed by a male 196 cm long. However, some males more than 210 cm long had testes weighing less than 300 g. Testes weight begins to increase sharply at 50- to 55-kg body weight and is strongly correlated with weight in larger animals. Males in the sample that weighed more than 70 kg (eight animals) had testes weighing more than a kilogram. The male with the third heaviest testes (2,017 g—heaviest testes for which body weight also available) weighed 80 kg; the heaviest male in the sample weighed 91 kg and had testes weighing 1,348 g. A rapid increase in testes weight (Figure 19) occurs at age 7 to 13 layers, with maximum size increasing until 12 to 16 layers. All animals with more than 14 layers had testes weighing 500 g or more. Again, there is wide variation in testes size relative to age. Part of the variation is ascribable to the considerable error in the estimate of number of dentinal layers (±2 layers for animals with more than 5 to 12 layers, more for older), but it must be concluded that there is probably about a 5-layer period during which the onset of puberty may

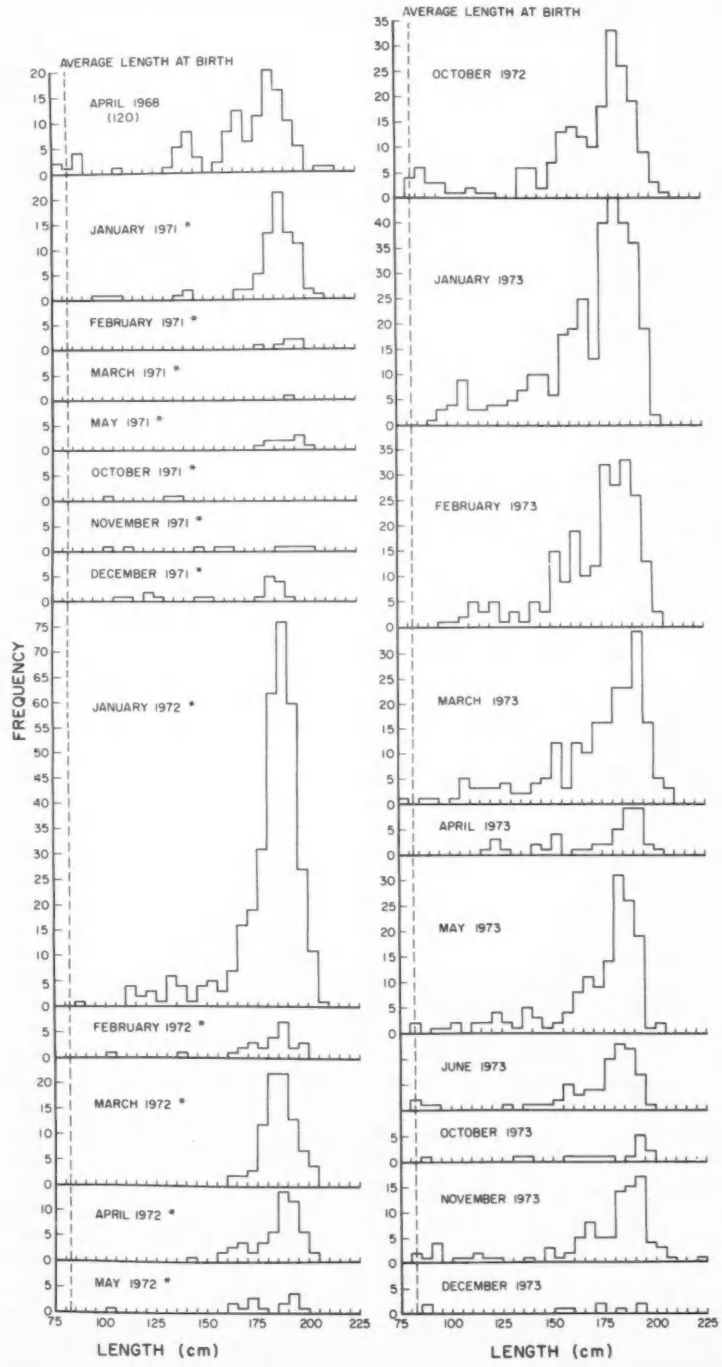

FIGURE 16.—Length-frequency distributions of postnatal female specimens of *Stenella attenuata*, 1968-73, by month.

take place (age about 7 to 12 layers) and that about 2 to 4 layers are required to attain "adult"

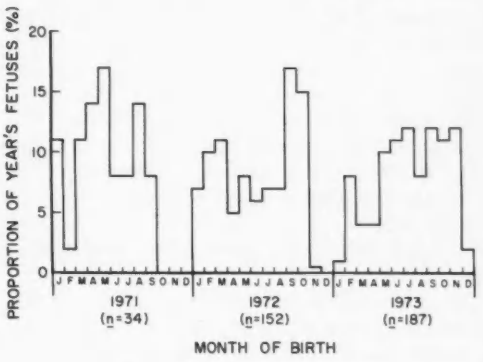

FIGURE 17.—Predicted month of birth for 373 fetuses of *Stenella attenuata*, based on fetal growth curve.

testes size (500 to 2,000 g). The third largest testes were possessed by an animal (202 cm long, 80 kg, discussed above) that had nonreadable teeth that were worn to the gum in all four tooth rows. Such tooth wear may be a correlate of relatively great age.

The diameter of the seminiferous tubules begins to increase rapidly at body length of about 155 to 170 cm (Figure 20), or at lengths about 15 cm shorter than those at which testes weight begins to increase. Tubule diameter is definitely correlated with body length until at least about 200 cm. The heaviest male (91 kg) had the largest tubules. The plot of tubule diameter on layers (Figure 21) indicates that the tubules enter a rapid development stage at 6 to 11 layers, before the onset of a rapid increase in testes weight (Figure 19). Asymptotic diameter is about 170μm and appears to be attained by 10 to 14 layers.

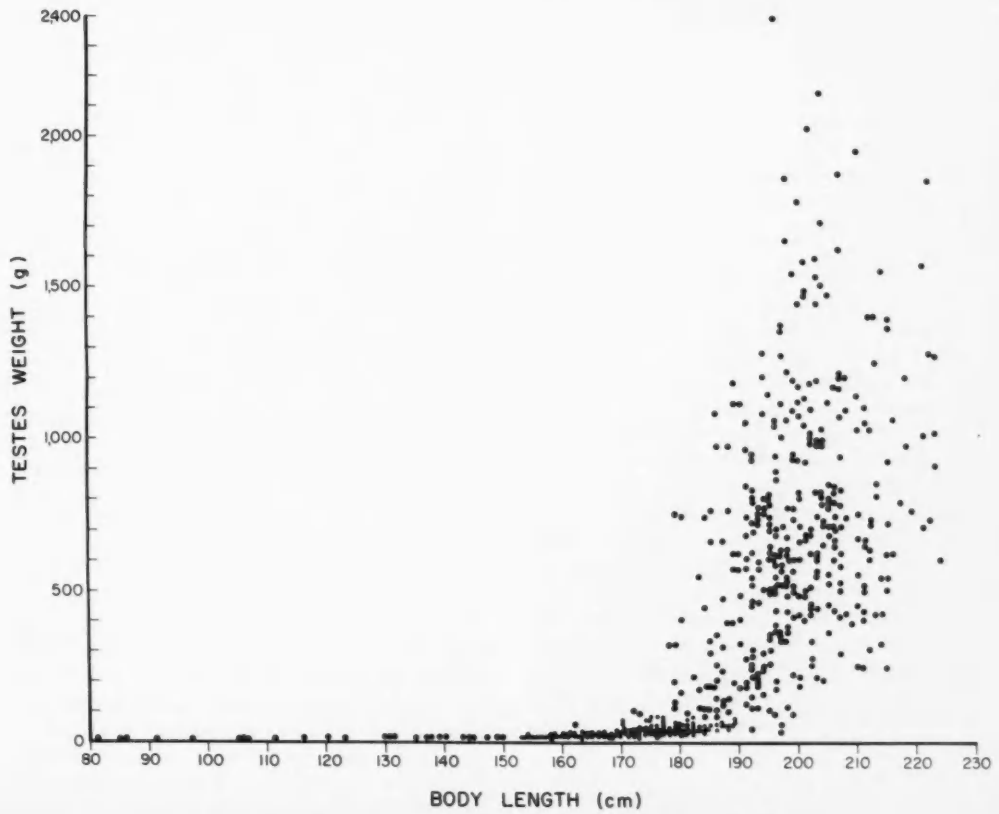

FIGURE 18.—Scatterplot of testes weight on body length in *Stenella attenuata*.

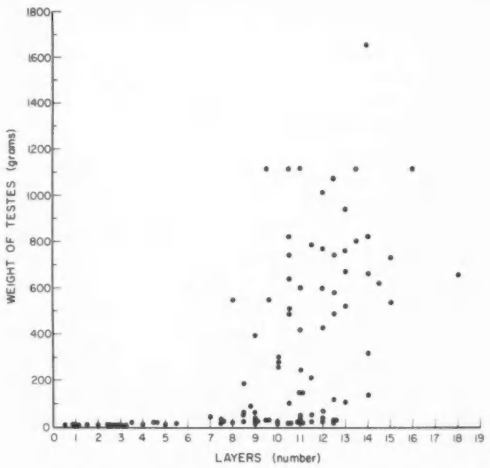

FIGURE 19.—Scatterplot of testes weight on number of postnatal dentinal layers in *Stenella attenuata*.

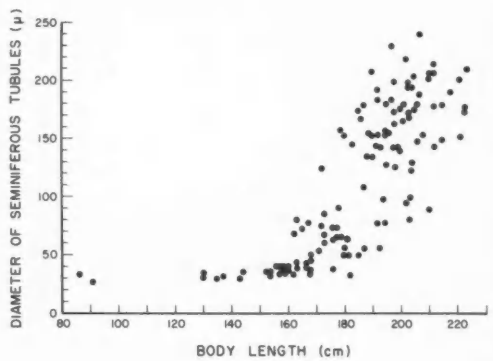

FIGURE 20.—Scatterplot of average diameter of seminiferous tubules on body length in *Stenella attenuata*.

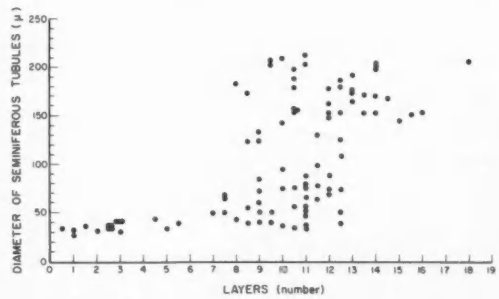

FIGURE 21.—Scatterplot of average diameter of seminiferous tubules on number of postnatal dentinal layers in *Stenella attenuata*.

Sperm in the epididymis were scored as "absent," "present in small numbers," or "copious" (easily seen in the histological sample without searching). The shortest individual with large numbers of sperm in the epididymis was 179 cm long. This animal weighed 62 kg. In animals larger than 180 cm and heavier than 58 kg, presence or absence of sperm in the epididymis bears little relationship to total length. Thirty-six large adults (>200 cm) were equally distributed among the three categories of no sperm, some sperm, and copious sperm.

The smallest testes bearing epididymis with sperm weighed 200 g, and the smallest testes with copious sperm weighed about twice as much. Some animals with testes heavier than 1.5 kg, however, had no sperm in the epididymis. The same pattern of wide variation is apparent in the relationship between epididymis code and layers. The youngest male with sperm in the epididymis had 9 layers. The youngest animal with copious sperm had 10 layers. After about 10 layers, there appears to be no relationship between age and presence or absence of large numbers of sperm.

In summary, the onset of puberty, as indicated by a rapid increase in diameter of seminiferous tubules and increase in testes weight, is at 7 to 12 layers (average ~9 layers; an estimate of ages at puberty) and at lengths of 155 to 170 cm and weights of 40 to 50 kg. Sexual maturity is attained about 2 to 4 layers later, at 10 to 14 layers, ≥180 cm, and ≥58 kg. The midpoint of the range of 10 to 14 layers, or 12 layers, may be taken as an approximation of average age at attainment of sexual maturity. Whether or not males at this point are "socially mature" (sense of Best 1969) can be determined only through behavioral studies. Average length of males 12 layers old is about 195 cm, and average weight is about 75 kg.

The Female

Attainment of Sexual Maturity

Harrison et al. (1972) described and figured the ovaries of *S. attenuata* (as *S. graffmani*). The ovaries weigh less than 0.5 g each at birth. Weight increases gradually to about 1.5 g at about age 6 to 8 layers (average ~7 layers; an estimate of age at puberty), when there is a sudden increase in average ovary size and weight due to presence of corpora of ovulation and/or pregnancy (Figure 22). This change comes at an

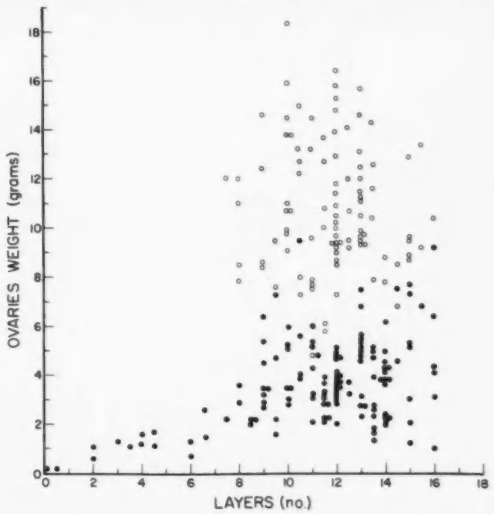

FIGURE 22.—Relationship between weight of ovaries and number of postnatal dentinal layers in *Stenella attenuata*. Open dots are females with a corpus luteum.

average total length of about 170 to 180 cm and weight of 50 to 60 kg (Figure 23).

Analysis of lengths of females with and without ovarian scars yields a more precise estimate of length at attainment of sexual maturity. The smallest of 1,410 specimens (160 cm long or longer) that possessed scars were two that were 167 cm long (one with a corpus luteum only and one with a corpus luteum and four corpora albicantia). The largest female with no scars was 193 cm long. The length-maturity curve is slightly asymmetrical, but a linear regression line through the nearly linear central portion ($M = 5.76L - 960.95$) estimates that average length at which scarring is first evident is 175.4 cm. This analysis probably underestimates length at attainment of maturity, because some of the small adults (170 to 180 cm) with many scars are those that have stopped growing at a shorter-than-average length. In other words, the left-hand portion of the frequency distribution of physically mature adults to an unknown extent artificially elevates the central portion of the length-maturity curve, making it asymmetrical.

An estimate of age and length at attainment of sexual maturity can also be derived directly from the smaller sample of females for which the number of tooth layers was determined. The youngest specimen exhibiting ovarian scarring had 7.5 layers. The oldest with no scarring had 12 layers. The estimated age at which 50% have scars is 9.14 layers ($M = 19.5t - 128.25$). Predicted length at this age is 181.6 cm (based on growth equation above). This estimate is less biased than the others above but based on much smaller samples, especially at the lower end of the layer-maturity curve.

Another estimate of length and age at first ovulation can be made by back extrapolation of a relationship between body length and number of corpora (including corpora lutea) in the ovaries (Figure 24). Length increases with corpora count until at least six to eight corpora have been accumulated, at about 183 to 190 cm. A fit of the data to the Laird growth model (above) yields the equation

$$L = 180.17 \text{ cm } \exp\{0.0541[1 - \exp(-0.2815C)]\},$$

where L = length in centimeters
C = number of corpora.

Back extrapolation of the curve to zero corpora yields an estimate of 180.2 cm. Predicted age from the growth equation is 8.74 layers.

An estimate of length at first conception can be made by calculating the average length of pregnant females with a corpus luteum only (indicating first pregnancy) and subtracting the growth that they can be assumed to have undergone during pregnancy. Fifty-four primiparous females averaged 181.7 cm in length (range 167 to 193 cm). Predicted age at that length is 9.17 layers. The average length of their fetuses was 372 mm. This length is attained by about the beginning of the sixth month of gestation. Using the growth equations above to predict growth during 6 mo for the various tooth-layering models and substracting the growth increment from 181.7 cm yields estimates of length at first conception ranging from 177.7 to 180.0 cm (number 4 in Table 2). The primiparous females in this sample, however, are only those that became pregnant at the first ovulation. This may cause the estimate to be an underestimate, because many females ovulate several times, and presumably continue to grow, before becoming pregnant the first time (see Ovarian Changes below).

The various methods of estimating age and length at attainment of sexual maturity yield estimates of varying accuracy (Table 2). The estimates based on tooth layers and length at first

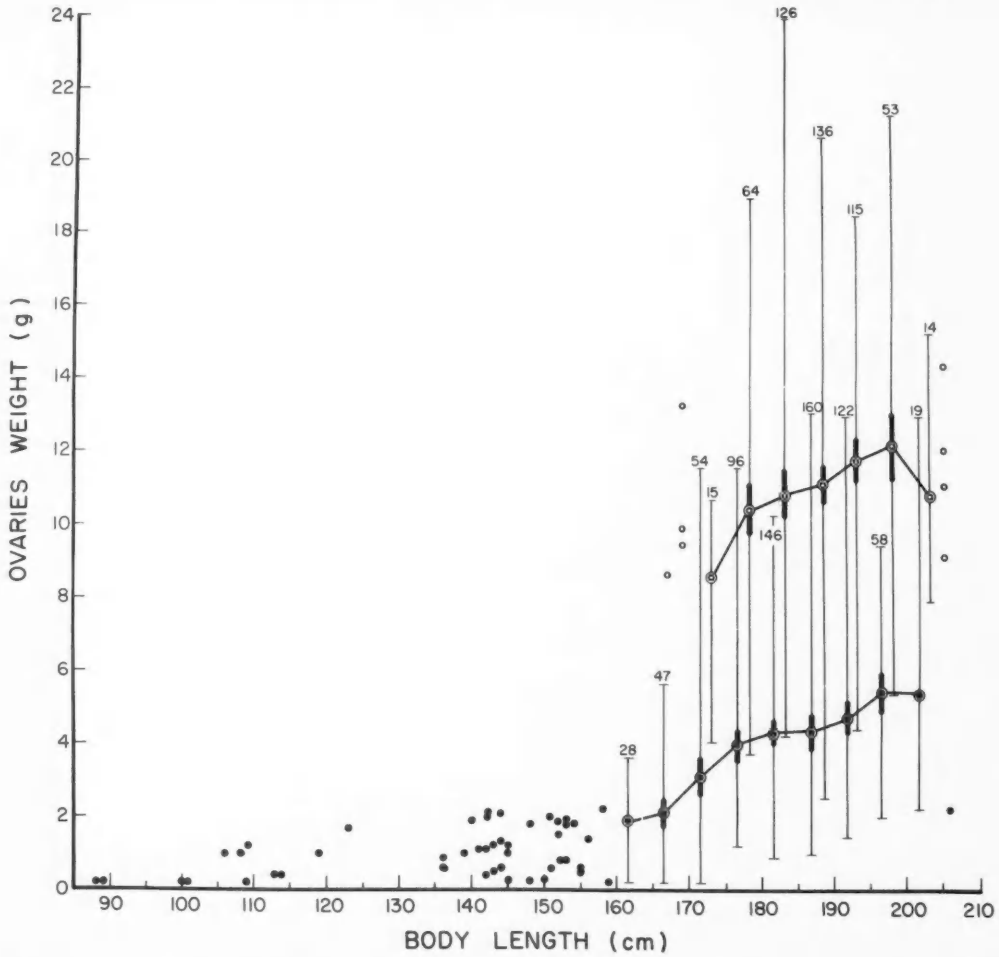

FIGURE 23.—Scatterplot of weight of both ovaries on body length in *Stenella attenuata*. Open dots represent females with a corpus luteum. For animals 160 cm or longer, where sample for 5-cm interval is 10 or more, means (circled symbols) and ranges are graphed and points are not plotted. Where the sample is ≥30, ± two standard errors are indicated by bars.

conception are the best of the four and probably bracket the true values. Under method number 3, age hypotheses numbers II and III are more probably correct than number I. Accordingly, we estimate that sexual maturity is, on the average, attained at 181 ± 1 cm and 9.0 (8.6 to 9.3) layers (5.1 to 8.3 yr, depending on the alternative layering hypothesis used).

An increase in size of Graafian follicles is another criterion of approaching sexual maturity. Diameter of the largest follicle also shows a sharp increase after 160 cm total length (Figure 25), concurrent with the increase in ovary weight (Figure 23). The largest follicle in immature females usually is less than 1 mm in diameter. The largest follicles in most ovaries containing scars are between 1 and 8 mm in diameter, but a few follicles (possibly cystic) as large as 10 to 16 mm in diameter were encountered.

Ovarian Changes in Adults

The analyses of ovarian changes are based on material collected through 1972. The corpus

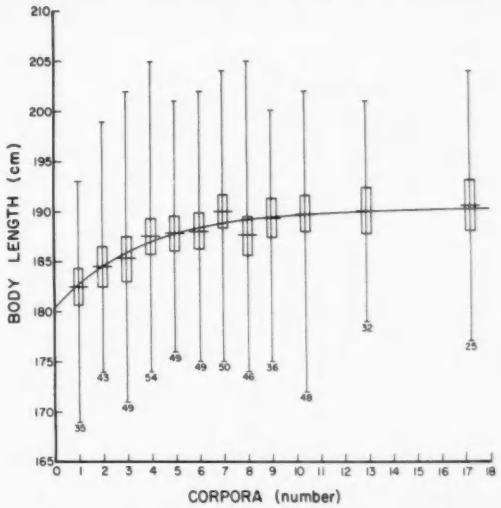

FIGURE 24.—Relationship between body length and number of corpora in *Stenella attenuata*. Average (bar), ± two standard errors (box), range (vertical line), and sample size shown.

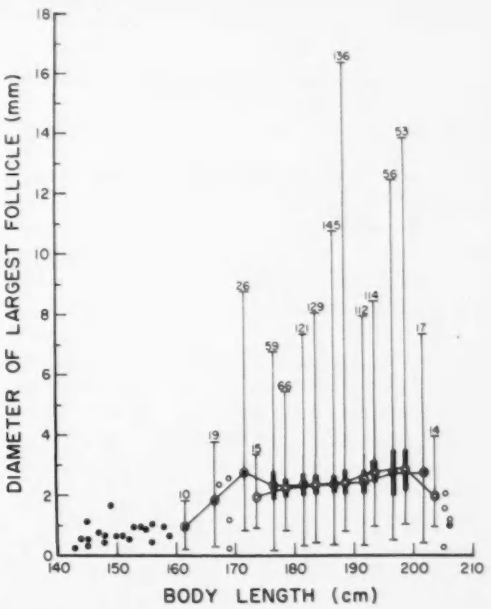

FIGURE 25.—Relationship between body length and diameter of the largest Graafian follicle in *Stenella attenuata*. Open dots represent females with corpus luteum. For length ≥160 and $n \geq 10$, means (circled symbols) and ranges shown. For $n \geq 30$, ± two standard errors are shown. Not included are 27 "senile" specimens with follicles <0.1 mm and five juveniles 88 to 122 cm with 0- to 1-mm follicles.

TABLE 2.—Results of analyses of length and age at attainment of sexual maturity in *Stenella attenuata*, with comments (in parentheses) on pros and cons of the methods. Lengths and layer counts predicted with the growth equations are in parentheses.

Analysis	Length (cm)	Layers (no.)	Age (yr), under hypothesis I	II	III
1. Length at which 50% have corpora (probable underestimate).	175.4	(7.66)	3.8	6.7	4.3
2. Number of tooth layers at which 50% have corpora (interpolation, but small sample sizes).	(181.6)	9.14	4.6	8.1	5.6
3. Back-extrapolation of corpora-length curve (large samples, but extrapolation).	180.2	(8.74)	4.4	7.7	5.2
4. Length at first conception under hypothesis: I	177.7	(8.17)	(4.1)	—	—
II	180.0	(8.57)	—	7.6	—
III	180.0	(8.57)	—	—	5.1
(includes only those that become pregnant at first ovulation; probable underestimate).					

luteum of pregnancy arises from the ruptured follicle and has an important secretory function in maintaining early pregnancy in all mammals and full gestation in most (Amoroso and Finn 1962). The gross and microscopic structures of corpora lutea in various delphinids, including *S. attenuata*, have been described by Harrison et al. (1972).

The corpus luteum decreases in size during gestation (Figure 26). Of 242 females with corpora lutea, 229 were pregnant. Eleven with fetuses less than 20 mm long (range 1 to 20 mm) had corpora with diameters of 23 to 29 mm (average 26.0 mm, SD 2.90). The mean diameter dropped sharply to 23.6 mm (range 21 to 27 mm, SD 2.27) in 17 females with fetuses between 20 and 100 mm (using Student's t, means are significantly different at $\alpha = 0.01$). This amounts to about a 32% decrease in luteal volume. Size of the corpus luteum continues to decrease at a slower rate, to 22.2 mm (range 19 to 28 mm, SD 1.79) in females with fetuses 700 to 825 mm (average length at birth is 825 mm) long, a further decrease in volume of about 15%. Luteal volume in females with near-term fetuses is only about half of that shortly after conception. Mean diameter in 10 females with fetuses longer than average birth length (825 mm) was 24.0 mm (range 20 to 26 mm, SD 2.21, greater than mean for 700 to 825 mm at $\alpha = 0.01$), a volume difference of about 38% more than for fetuses 700 to 825 mm long. Delayed regression (or re-enlargement) of the corpus luteum is apparently correlated with greater-than-average length at birth.

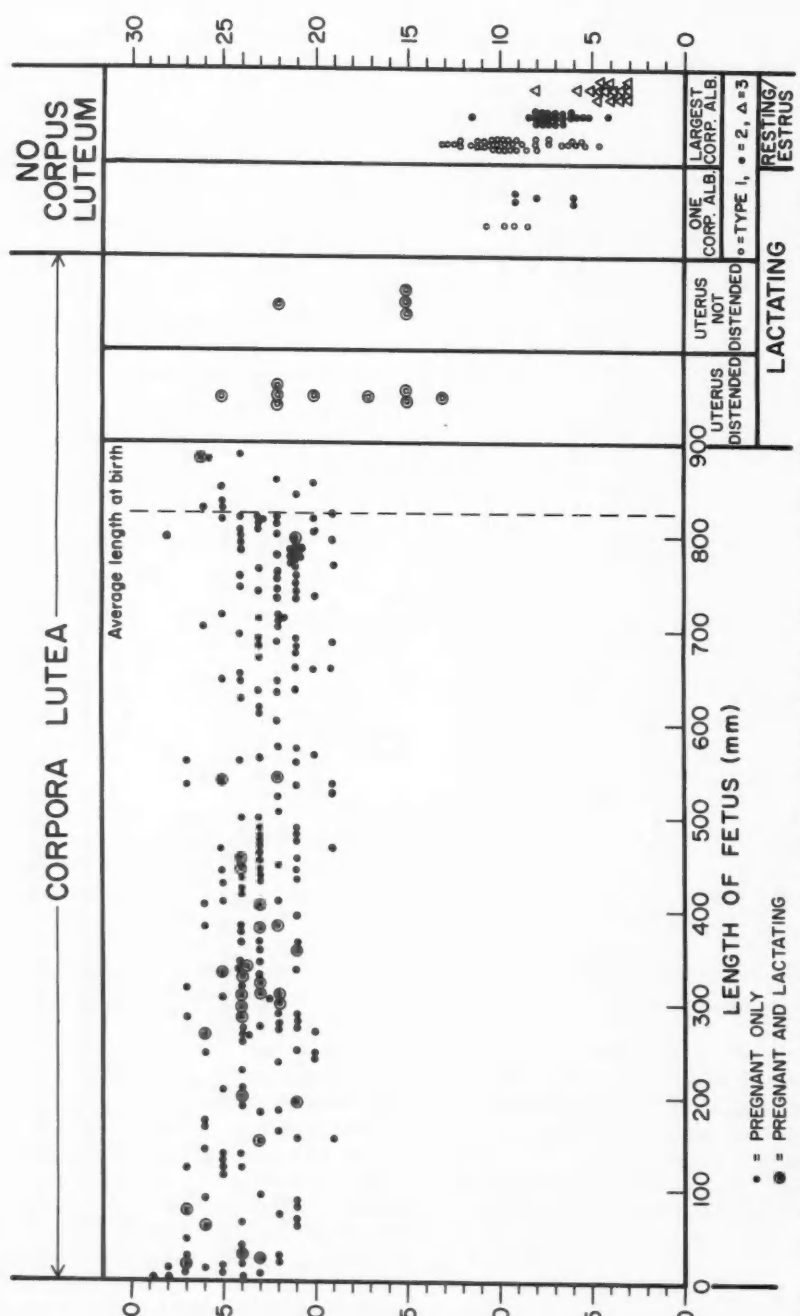

FIGURE 26.—Average diameter of corpus luteum in pregnant, lactating, and resting females of *Stenella attenuata*. Aberrant corpora (cystic, double, etc.) are not included.

Nine obviously postpartum females had corpora lutea 13 to 25 mm in diameter (Figure 26). Four lactating females with uteri not obviously distended had corpora lutea in the same size range. Average luteal volume in these lactating animals was less than half of that in animals at parturition. Some of these 13 cases may represent miscarriages.

The corpus luteum of pregnancy shrinks still further during the suckling period, losing its glandular appearance and becoming a corpus albicans. Nine of 197 lactating females without corpora lutea each had a single corpus albicans, which must represent the regressed corpus luteum of the first pregnancy. These corpora (Figure 26) were approximately spherical and 5.9 to 10.6 mm in diameter (average 8.5 mm). The lower end of this range—about 6 mm—must approximate the limit of regression during the suckling period (about 11.2 mo; see below). The small number of lactating females with corpora lutea (13) compared to the number with only copora albicantia (197) indicates that initial regression following parturition must be very rapid, perhaps occurring in less than 15 days. Still further regression in size and histological structure of the corpus albicans of pregnancy probably occurs. Many adult females have a large corpus albicans (in most cases, one of several) between 3 and 6 mm in diameter (Figure 26) with greatly degenerated structure. Unless these corpora all represent ovarian events not resulting in pregnancy, i.e., the females are all completely barren, the corpus albicans of pregnancy must decrease in diameter during a resting period following a pregnancy, to possibly as little as 3 mm.

Multiple corpora lutea are uncommon in *S. attenuata*. They were encountered in only 2 out of 258 females with corpora lutea. One of these was pregnant with twin fetuses (males, 83 and 86 mm) in the left horn of the uterus. The left ovary contained two corpora lutea of approximately equal size, each possessing a surface scar of ovulation, together with seven corpora albicantia visible on the surface. The right ovary was devoid of scars. Another female with two corpora lutea had a 592-mm fetus (male) in the left horn of the uterus. The left ovary looked very much like that of the specimen with twin fetuses, having two corpora lutea of approximately equal size and eight corpora albicantia on the surface. Neither corpus luteum bore a discernible surface scar. The right ovary was unscarred. There are two possible explanations for the presence of two corpora lutea in this specimen: 1) one of them was an accessory corpus, or 2) one of a pair of twin fetuses was aborted during early pregnancy. In any case, the incidence of multiple corpora lutea is very low in *S. attenuata*, less than 1% in the sample examined. This is in sharp contrast to some other cetaceans, in which rates of presence of accessory corpora range to 15.6% (*Delphinapterus leucas* —Brodie 1972). The contribution of double and accessory corpora lutea to the accumulation of corpora albicantia can be considered to be negligible in *S. attenuata*.

Corpora albicantia in *S. attenuata* represent both regressed corpora lutea of pregnancy and regressed corpora of ovulations that do not result in pregnancy. This conclusion is based on the accumulation rate of corpora albicantia and on the estimate of the mean length of the calving interval (see below). We were not, however, able to differentiate between small regressed corpora lutea and regressed corpora of ovulation. This impasse, also encountered by workers dealing with other cetaceans (Harrison et al. 1972) is caused by the wide and largely discordant variation in size, shape, surface texture, and internal structure and color of the corpora albicantia. If one looks at enough corpora, it is possible to find corpora with these characters in almost any combination of expressions.

Harrison et al. (1972) found no more than six corpora albicantia in the ovaries of any *Stenella* female. In the present sample, however, nearly half (44%) of the females had more than six corpora, including the corpus luteum. Fifty-five females of 1,131 had 15 or more corpora; one had 28 (Figure 27). Three thousand five hundred and two corpora from ovaries of 530 females were scored to six categories. These categories are somewhat arbitrary in view of the continuity of regression and the wide variation discussed above, but, nonetheless, they are useful in analyzing the course of regression. The numbers and proportion of total corpora complement represented by each of these categories varies with the total number of corpora (Table 3, Figure 28). The categories were defined as follows:

Type 1. Surface raised, smooth or slightly wrinkled. Looks externally like a small corpus luteum. Cortex white or yellow, with obvious remnants of vascularization. Center solid or loosely constructed, consisting mainly of white

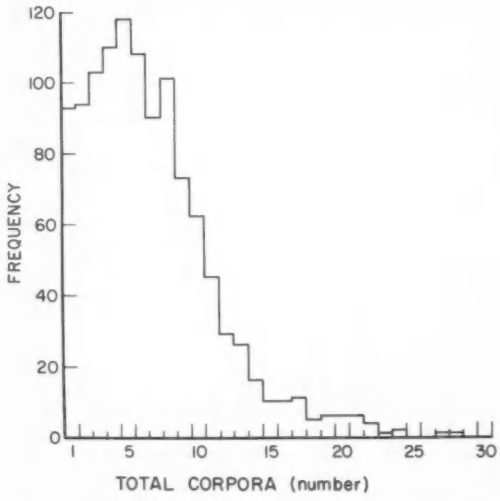

FIGURE 27.—Frequency distribution of corpora count in 1,131 females of *Stenella attenuata*.

connective tissue, 3.5 to 15.5 mm in diameter, average 7 mm. These corpora almost certainly are nearly all regressed corpora lutea. Four hundred fifty-six were encountered (13.2%). Females with two or more corpora have, on the average, about one Type 1 corpus (Figure 28), although as many as five may be present (Table 3).

TABLE 3.—Types of corpora present in ovaries of *S. attenuata* in relation to total corpora. Averages in Figure 28.

Total number of corpora (including corpora lutea)	Sample size (no.)	Range of number of each type of corpus albicans—Type:					
		1	2	3	4	5	6
1	35	0-1	0-1	0	0	0	0
2	42	0-2	0-2	0-1	0-1	0-1	0
3	48	0-3	0-3	0-2	0-1	0	0
4	53	0-3	0-4	0-3	0-1	0-2	0
5	49	0-5	0-4	0-5	0-2	0-2	0
6	49	0-5	0-4	0-6	0-3	0-1	0
7	50	0-5	0-5	0-6	0-3	0-2	0-1
8	46	0-5	0-6	0-7	0-2	0-4	0
9	36	0-2	0-5	2-9	0-4	0-3	0-1
10-11 (average 10.4)	48	0-4	0-5	3-10	0-2	0-2	0-1
12-14 (average 12.9)	32	0-2	0-5	3-14	0-3	0-4	0-3
15-27 (average 17.2)	25	0-4	0-5	7-19	0-2	0-9	0-1
Total	513	0-5	0-6	0-19	0-4	0-9	0-3

Type 2. Surface raised and wrinkled. Interior white to yellow, often with traces of luteal cortex and vascularization. Center solid or loosely constructed, consisting mainly of white connective tissue. Definitely less integrated in structure than Type 1 (above). Diameter 3.0 to 12.0 mm, average 6 mm. The evidence on accumulation rate (below) suggests that these corpora are probably a mixture of regressed corpora lutea and corpora of ovulation. We found 787 of this type (22.5%). The number of Type 2 corpora is relatively constant in females with three or more corpora, at about one and one-half (Figure 28) with a

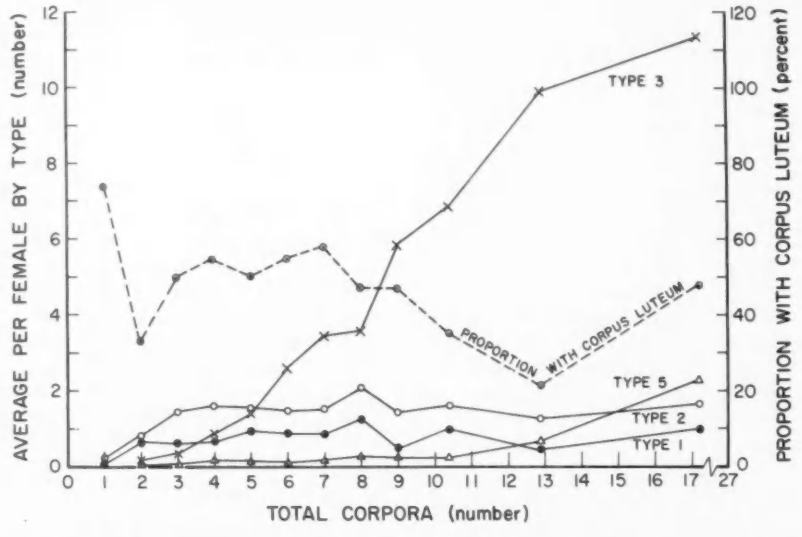

FIGURE 28.—Relationships between numbers of corpora of various types and total number of corpora in ovaries of females of *Stenella attenuata*. Ranges and sample sizes in Table 4.

range of 0 to 6 (Table 3). This number is tightly correlated with the number of Type 1 corpora (Figure 28), indicating that there may be some overlap in the classification criteria for these categories.

Type 3. Surface usually not raised; scar usually smaller than Type 2 and heavily wrinkled. May be pedunculate and flattened. May be flattened against the surface or may run deep into the ovary. Interior consists of white connective tissue. May have yellow "stains" around the white center. When many corpora are present, some of this type may be present but not apparent at the surface. Diameter 2.0 to 8.5 mm, average 3.5 mm. This is a catch-all category for all small compact corpora with surface scars and internal structure. It probably includes both regressed corpora lutea and corpora representing ovulation and other events. We found 1,999 corpora of this type (57.1%). The number increases steadily with total corpora number (Table 3, Figure 28), while the numbers of Types 1 and 2 corpora remain constant, indicating that Types 1 and 2 corpora regress into and accumulate as Type 3 corpora. This is assuming, of course, that total corpora count is related to age (see below).

Type 4. Thin, flattened against the surface of a new corpus luteum. Two to 15 mm in diameter. These are Types 2 and 3 corpora that cannot be allocated to those categories because of distortion caused by the corpus luteum. One hundred were encountered (2.9%).

Type 5. Surface trace very slight or apparently absent. Interior deep yellow or orange, with no concentrated connective tissue or apparent internal structure. Diameter 0.5 to 5.5 mm, average 2 mm. Harrison et al. (1972) have suggested that this type of corpus is the end result of regression of an atretic lutealized follicle. We encountered 149 (4.3%).

Type 6. A small surface scar with no discernible internal structure. Two to 5 mm in diameter. Only 11 corpora of this type were encountered (0.3%). They may represent extremely regressed corpora of other types or may originate from different ovarian events.

Types 1, 2, and 3 comprise a series of increasing regression and/or decreasing complexity of original structure, and it is probable that regressing corpora lutea pass through these types or stages. The shapes of the diameter frequency distributions (Figure 29) suggest that corpora albicantia regress to an average size of about 3 mm in diameter and then persist and accumulate at that size for at least part of the remainder of the life of the female. The skewness of the aggregate distribution (sum Types 1, 2, and 3 in Figure 29) becomes even more significant when one considers that the volume of the corpus decreases as the cube of the diameter. On a volume scale, the left

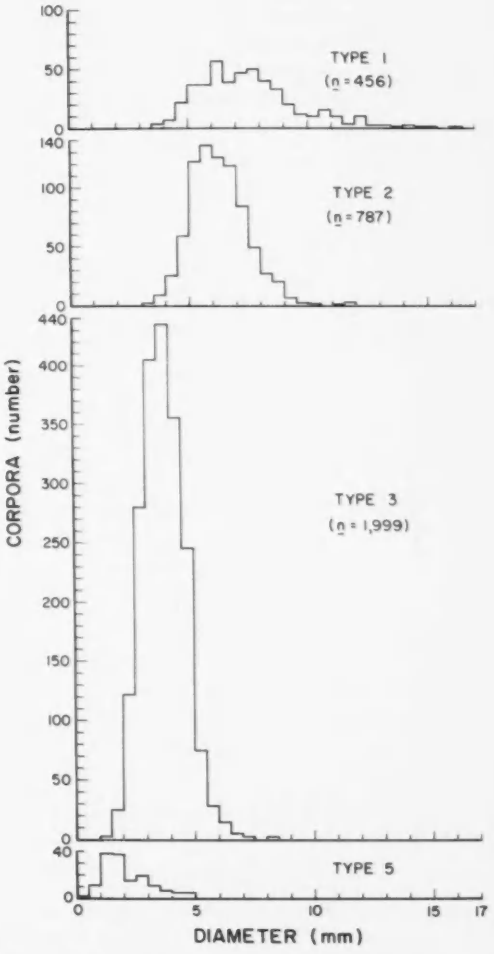

FIGURE 29.—Frequency distribution of diameter of Types 1, 2, 3, and 5 corpora albicantia in *Stenella attenuata*.

side of the curve would be steeper and the right side less steep.

Consideration of the relative rates of deposition of corpora in the left and right ovaries is important to the question of persistence of corpora. The distribution of corpora between left and right ovaries is related to the number of corpora present (Table 4). The first corpus occurs in the left ovary about 94% of the time. Subsequent corpora occur in the same ovary as preceding ones at about the same rate (~95%), causing a gradually increasing percentage of animals with corpora in both ovaries, until about 10 to 11 corpora have been deposited, when emphasis switches sharply to the opposite ovary (left or right). All females with 15 or more corpora (27 specimens) had corpora in both ovaries.

A group of 15 seemingly postreproductive females was encountered. These specimens had very small, obviously regressed ovaries with 10 to 15 Type 3 or smaller corpora albicantia (Figure 30). They had no corpora lutea or Type 1 corpora

TABLE 4.—Location of corpora (corpora lutea and corpora albicantia) in ovaries of 488 specimens of *Stenella attenuata*.

Corpora (no.)	Sample size (no.)	Location of corpora		
		Left ovary only (%)	Right ovary only (%)	Both ovaries (%)
1	31	93.6	6.4	—
2	40	85.0	7.5	7.5
3	44	86.5	4.5	9.0
4	53	88.7	1.9	9.4
5	47	78.8	2.1	19.1
6	48	75.0	4.2	20.8
7	45	73.4	2.2	24.4
8	41	61.0	2.4	36.6
9	34	70.6	2.9	26.5
10-11	47	46.8	2.1	51.1
12-14	31	6.5	0.0	93.5
15-27	27	0.0	0.0	100.0
Total	488			

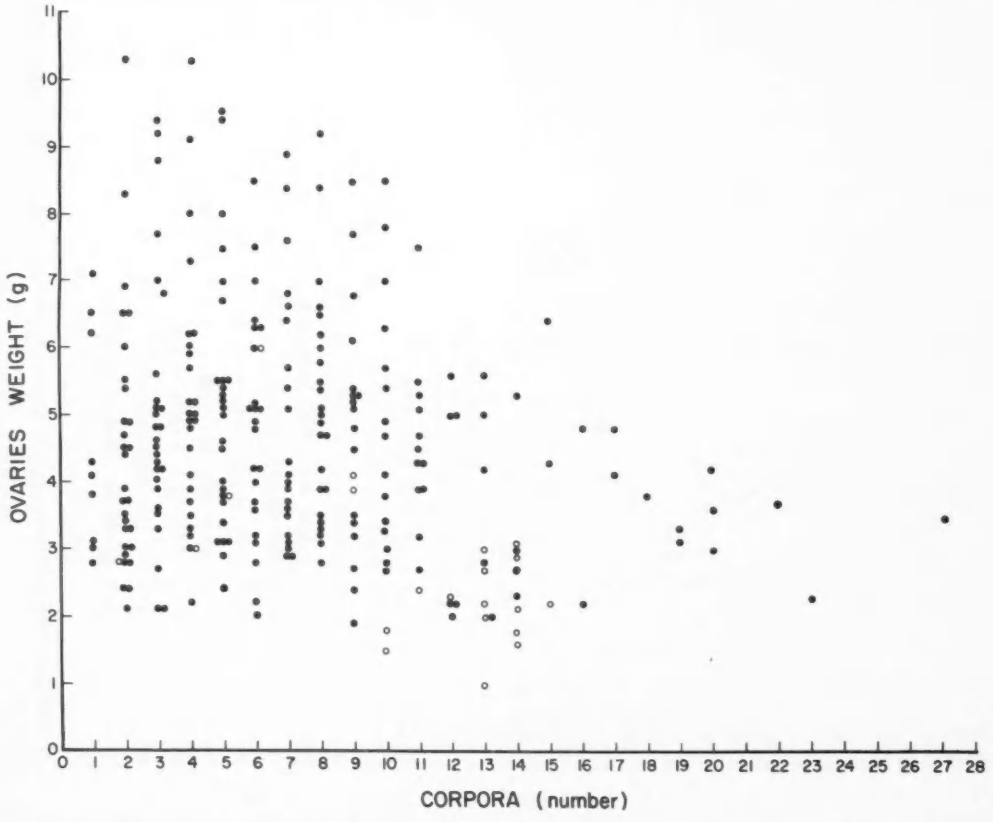

FIGURE 30.—Scatterplot of ovaries weight on number of corpora in *Stenella attenuata*. Females with corpus luteum not included. Open dots are females with no Type 1 or 2 corpora albicantia.

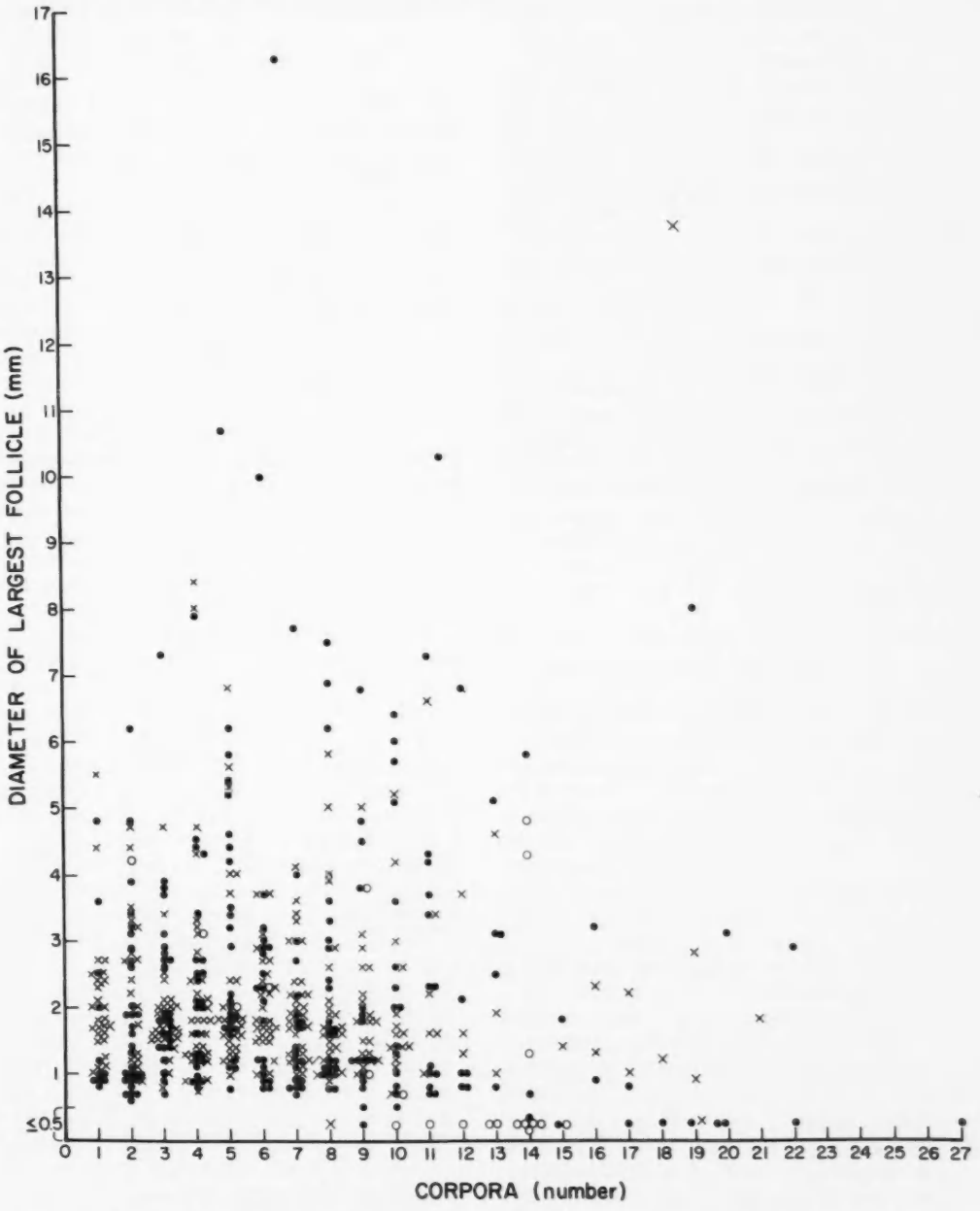

FIGURE 31.—Scatterplot of diameter of largest follicle on number of corpora in *Stenella attenuata*. Females with corpus luteum indicated with ×. Open dots are females with nor corpus luteum or Type 1 or 2 corpora albicantia.

albicantia. They also typically had very small Graafian follicles (Figure 31). A consideration of these females bears on the question of persistence of corpora albicantia. Sergeant (1962) encountered similar females in *Globicephala*. They comprised about 5% of adult females. He called them "senile" and concluded that the ovarian scars in these animals represent some residual subset of the maximum complement of corpora of pregnancy, ovulation, and other events. He implied that they probably are the corpora of pregnancy, since those corpora are larger at the outset and presumably less likely to regress to the point of macroscopic disappearance. The ovarian data for *S. attenuata* do not support this hypothesis of disappearance of some corpora in regressed ovaries. The regressed ovaries have 10 to 15 corpora (Figures 30 and 31). The ovaries of other, still reproductive females are larger and have 16 to 27 corpora, although follicles are typically smaller than in reproductive females with fewer corpora (Figure 31). Three alternative hypotheses explain this apparent dichotomy in females with 10 or more corpora:

1. The usual maximum number of corpora is about 21, and some corpora disappear in postreproductive females, i.e., the "senile" group in Figure 30 properly belongs at the far right side of the plot at the end of a downward trend in ovary weight (the hypothesis of Sergeant 1962).
2. Corpora are laid down at about the same rate in all individuals, but some become postreproductive at about 10 to 15 corpora while others continue to accumulate corpora (16 to 27) until a greater age, i.e., the corpora scale in Figure 30 is effectively an age scale. Under this hypothesis, corpora do not disappear.
3. Corpora are accumulated at rates varying widely among individuals, but the typical maximum complement is 10 to 15 corpora, i.e., the reproductive females with more than 15 corpora in Figure 30 properly belong in the body of the distribution in the left two-thirds of the plot. A possible explanation for widely varying rates of accumulation is that some females are more fecund and the senile period is reached with some maximum number of pregnancies, so that the varying ratios of corpora of pregnancy to corpora of ovulation may produce the apparent dichotomy. Sergeant (1973) found greatly varying individual rates of ovulation in the white whale, *Delphinapterus leucas*.

In order to examine these alternative hypotheses, the females in Figure 30 and 31 with 10 or more corpora were examined in three groups—A, B, and C:

A. 10 to 15 corpora, reproductively active (corpus luteum and/or Types 1 and 2 corpora albicantia).
B. 16 or more corpora, reproductively active.
C. 10 to 15 corpora, postreproductive (ovaries regressed, no corpus luteum or Types 1 or 2 corpora albicantia).

The three groups were compared in terms of corpora count, weight of ovaries, size of largest follicle, number of dentinal layers, total length, and relative corpora counts in left and right ovaries (Table 5). Only nonpregnant females were included in the sample for ovary weight. Follicle size was examined separately for pregnant and nonpregnant animals.

Ovary weight and follicle size for nonpregnant animals decline progressively from A to C. This is

TABLE 5.—Characteristics of females of *Stenella attenuata* in groups A, B, and C (see text).

Item	A	B	C
Corpora (no.)			
Sample size	67	24	15
Average	11.2	18.9	12.9
Range	10-15	16-27	10-15
SD	1.41	2.56	—
Ovary weight (g) (nonpregnant)			
Sample size	44	13	15
Average	4.4	3.6	2.2
Range	2.0-8.5	2.2-4.8	1.0-3.1
SD	1.61	0.81	0.59
Largest follicle (mm) (nonpregnant)			
Sample size	27	13	<14
Average	2.9	1.5	<0.5
Range	<0.5-10.3	<0.5-8.0	0.5-4.3
SD	2.53	2.35	—
Layers (no.)			
Sample size	30	18	7
Average	13.1	13.1	13.2
Range	10.0-16.0	11.0-15.0	11.5-16.0
SD	1.39	1.31	1.52
Length (cm)			
Sample size	67	24	15
Average	190.1	190.3	187.0
Range	172-202	177-204	179-192
SD	6.43	6.78	3.54
Left/right ovary			
Sample size	65	23	15
Average in right (%)	24	33	29
Left/right (no./no.)	548/178	291/144	—

a requirement of hypothesis 1, above, but does not eliminate hypotheses 2 and 3.

The three groups do not differ in average estimated number of tooth layers. This may, in part, be due to the difficulty of accurately counting the innermost layers in teeth with more than 12 layers (the number of layers is probably underestimated by as much as one-third in teeth with large amounts of convoluted secondary dentine), but careful comparison of the teeth of the three groups in terms of other features presumably correlated with age, such as tip wear, degree of closure of the pulp cavity, and amount of secondary dentine does not indicate that any group is older than any other. This evidence is against hypothesis 1, which requires that group C be older than A, and hypothesis 2, which requires that B be older than A and C.

Groups A and B have reached asymptotic length (~190 cm). The animals in group C averaged about 3 cm less. A statistical comparison of A with B using Student's t indicates that the difference is significant at $\alpha = 0.05$. These results do not eliminate or support directly any of the hypotheses. Since A, B, and C are about the same age, the length data indicate that asymptotic length may be less for females that become senile with 10 to 15 corpora. This indirectly supports the idea of considerable individual variation in life history.

The most convincing evidence against hypothesis 1 has to do with number of corpora in right versus left ovaries. If the emphasis in corpus deposition shifts from left to right at about 10 corpora, and if group C regresses from group B (animals with about 20 corpora) losing about 6 corpora in the process, then group C should have about equal numbers of corpora in the right and left ovaries. If most corpora of ovulation come in early reproductive life (as data analyzed below indicate) and, as suggested by Sergeant (1962), are more likely to disappear than corpora of pregnancy because of smaller initial size, then the regressed group C should have, on the average, more corpora on the right than on the left, because most of the corpora of pregnancy would be in the right ovary. Forty-one percent of the corpora in 14 individuals having 18 to 22 corpora (average 19) were on the right. Only 29% of the corpora in group C were on the right. The difference between C and A (29 and 24%) can be accounted for simply by the difference in average total corpora count (12.9 and 11.2). These results eliminate the hypothesis (number 1 above) of loss of corpora with regression of ovaries.

The various lines of evidence largely speak against hypotheses 1 and 2 and support hypothesis 3, that of great individual variation in life history and of persistence of corpora albicantia. This is in line with findings by some other workers in small cetaceans (Sergeant 1962, 1973; Brodie 1971).

The data on the relationship of percent occurrence of corpora lutea to number of corpora (Figure 28) also support the hypothesis of widely varying rate of accumulation of corpora albicantia. After stabilization at about 50% at 3 to 4 corpora, the rate declines after 8 to 9 corpora to 20% at 13 corpora; but the rate for females with 17 to 27 corpora is again 50%. Assuming that fecundity is inversely related to age, this pattern suggests that the females in the 17 to 27 group are about the same age as those in the 3 to 9 group.

Ovulation Rate

Even assuming that corpora albicantia persist and represent various ovarian events, estimating average rates of accumulation is difficult because of 1) the above-mentioned unreliability of age estimates based on more than 12 tooth layers, 2) the evident individual variation in accumulation rate, and 3) change in ovulation rate during the reproductive span. All of these factors must contribute to the scatter in a plot of corpora number (including corpus luteum) on estimated age (Figure 32). Several workers have pointed out that cetacean ovaries often contain two or more corpora of the same size and same stage of regression. It has been suggested that these are the result of multiple infertile ovulations or lutealization of atretic follicles in newly mature animals (Harrison et al. 1972). Many in the present series of ovaries had two or more corpora (of Type 1 or 2) that were very similar in size and structure and must have resulted from nearly contemporaneous events. One probable multiple ovulation is apparent in Figure 32. This female, field number CWOR8, possessed 7 or 8 well-defined layers in its teeth. In spite of its extreme youth, it had a small corpus luteum, three Type 1 corpora, two Type 2 corpora, one Type 3 corpus, and one Type 4 corpus. The uterus was empty, and there was no milk in the mammaries. The animal could not have been reproductively active for more than about a year, but had already experienced eight

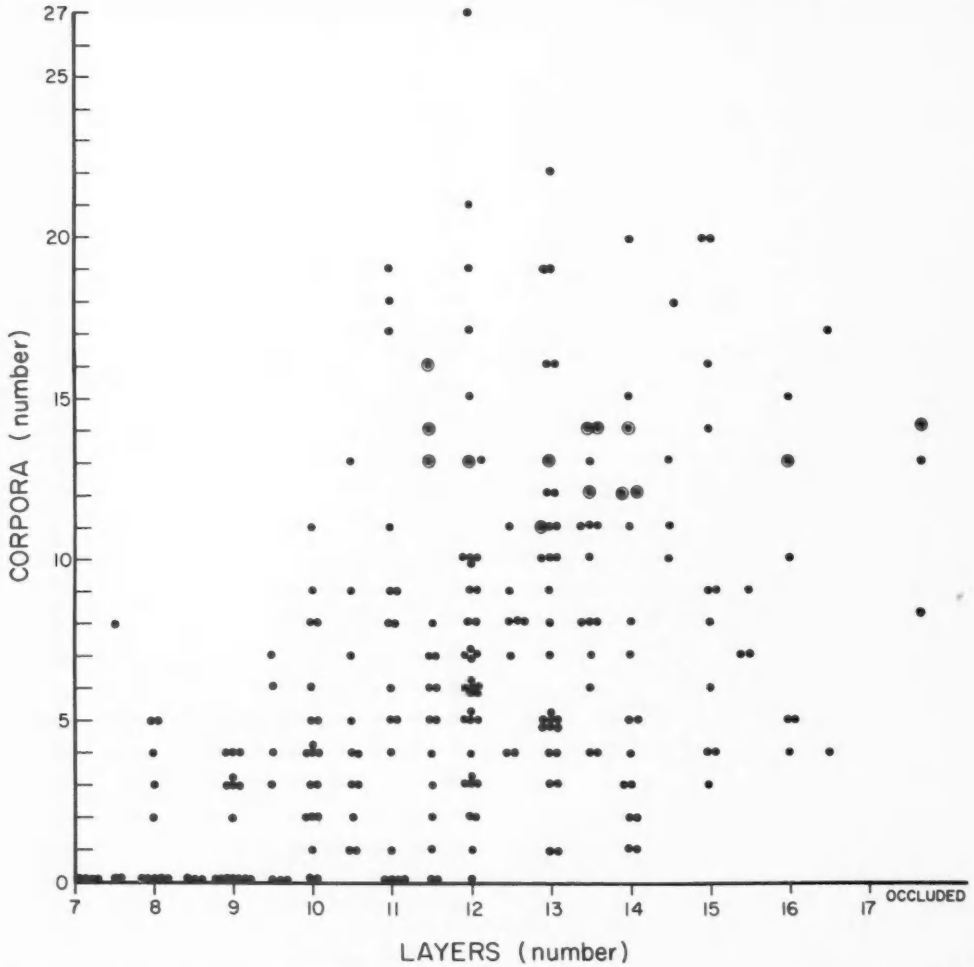

FIGURE 32.—Scatterplot of number of corpora on number of postnatal dentinal layers in *Stenella attenuata*. Circled symbols are senile females [shriveled ovaries with no corpus luteum or Type 1 or 2 corpora albicantia].

apparently nonreproductive ovarian events that resulted in corpora belonging to all of the types through which a corpus luteum must pass during regression to a small corpus albicans.

Calculation of average ovulation rates from the data in Figure 32 must take into account individual variation in age at first ovulation. The females in Figure 32 were grouped into 10 one-layer intervals beginning with 7.5 layers (Table 6). The average reproductive age in interval p was calculated as

$$\bar{A} = \left(\sum_{i=1}^{p} a_i b_i \right) \div c,$$

where a_i = % maturing in ith interval (% mature in i minus % mature in i - 1)
b_i = average reproductive age in interval p of females mature in i
c = % mature in interval p.

Average reproductive age in the ith interval of

TABLE 6.—Average reproductive ages and corpora counts of females of *Stenella attenuata* used in estimating ovulation rate based on corpora and tooth layers.

Layers (no.)	Sample (no.)	Proportion mature (%)	Average reproductive age of mature (layers)		Average corpora (no.)	
7.5- 8	13	46.2	0.50		4.50	
8.5- 9	18	44.4	1.56	1.43	3.25	4.21
9.5-10	24	79.2	1.67		4.53	
10.5-11	25	84.0	2.56		6.42	
11.5-12	52	94.2	3.25		8.35	
12.5-13	36	100.0	4.05		8.92	
13.5-14	31	100.0	5.06		8.71	
14.5-15	15	100.0	6.07		10.87	
15.5-16	7	100.0	7.08	6.60	9.86	10.45
>16	3	100.0	8.09		9.75	
Total	224					

Note: Teeth of all available females with more than 12 corpora were sectioned, while only a nonselective subsample of females with fewer corpora were included. The effect on estimate of average reproductive age is negligible, since nearly all had 11 or more layers.

females maturing in i was set at 0.50 layers. Because of small sample sizes, the first three intervals and the last three were pooled. The results show an increase in average corpora count (number of ovulations) with reproductive age (Figure 33). A curvilinear fit to the interval means, using a power model forced through the origin, fits well and indicates that ovulation rate is higher in animals of reproductive age 0-2 layers than in older animals. The breaking point seems to come at about 12 layers, when about 6 corpora have been accumulated and rate appears to become nearly constant. Average ovulation rates estimated from the curve are about four during the first layer, two during the second, and about one per layer thereafter.

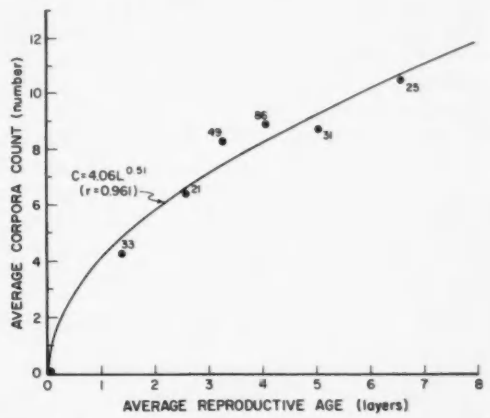

FIGURE 33.—Relationship between average number of corpora and average reproductive age (in layers) in *Stenella attenuata*.

Calving Interval

The pattern of reproduction definable with the methods used here consists of three phases: pregnancy, lactation, and a period of inactivity and/or estrus called here "resting/estrus." The length of pregnancy was estimated above as 11.5 ± 0.2 mo. We estimated length of lactation in three ways, based on 1) stomach contents of calves, 2) numbers of lactating females and calves, and 3) ratio between numbers of lactating and pregnant females.

The forestomachs of 45 calves less than 150 cm long were opened and examined by eye for presence of milk. Twenty-one were empty. The stomachs of four calves 120 to 130 cm long contained both milk and solid food (fish and/or squid). Stomachs of 8 smaller calves (80 to 115 cm) contained only milk, and 12 of the larger calves (130 to 150 cm) apparently contained only solid food. About 130 cm appears to be the length at which effective weaning occurs. The estimated time required to grow to 130 cm is 9.4 mo (based on growth curve above). This estimate is not very reliable for two reasons: the sample is small, and small amounts of milk could be present and undetectable by eye, i.e., suckling could continue at a low level after the effective shift to solid food. The estimate can, however, be considered to be a probable lower bound on length of lactation.

A second estimate is based on the assumptions that 1) a suckling calf exists for each lactating female and 2) the samples of specimens are unbiased with respect to suckling calves and lactating females. Given these assumptions, the length at which the cumulative frequency of calves in a sample equals the number of lactating females should be the average length at weaning. This length in eight variously sized, 1-mo "random" samples of calves and females ranged from 125 to 145 cm (Table 7). The aggregate estimate for the eight samples pooled (320 lactating females) is 137 cm. Average age at 137 cm is estimated at 1.94 tooth layers, or (assuming two layers accumulated during first year) 11.6 mo. If calves were overrepresented in the samples, this would be an underestimate. If they were underrepresented, it would be an overestimate. It would be an overestimate if the assumption that the number of lactating females equals the number of nursing calves were not valid. The assumption is not valid if the mortality of nursing calves is

TABLE 7.—Length at which cumulative frequency of calves equals the number of lactating females in eight 1-mo samples of *Stenella attenuata*.

Sample (mo)	Lactating females (no.)	Length (cm) at which cumulative frequency of calves = no lactating females
Oct. 1972	51	132
Jan. 1973	65	125
Feb. 1973	50	144
Mar. 1973	48	136
Apr. 1973	13	142
May 1973	32	142
June 1973	18	145
Nov. 1973 (Oct. 28-Dec. 11)	43	142
Total	320	137

higher than that of lactating females and lactation continues after death of a nursing calf.

A third estimate of length of lactation was derived from the ratio of lactating to pregnant females. This analysis included all the material from 1971 and 1972, when only adult females were sampled, as well as the material included in the calf-lactating female analysis above. Females both lactating and pregnant were included in both categories. The assumption is made that samples were unbiased with respect to relative representativeness for lactating and pregnant females. The ratio was 0.95 in the 1971 sample (86 adult females), 1.00 in 1972 (455), 0.96 in 1973 (573), and 0.97 for the pooled samples (n = 1,114; Table 8). The ratio of lactating to pregnant should equal the ratio of the lactation period to the gestation period. Gestation is 11.5 mo, therefore lactation is by this method estimated at 0.97 times 11.5 mo, or 11.2 mo. Estimated length at this age is 135.5 cm.

The three estimates of 9.6, 11.6, and 11.2 mo are based on largely independent assumptions and are close enough to each other to indicate that length of lactation is almost certainly between 9 and 12 mo. Of the three, the central estimate, 11.2 mo, is best in terms of sample size and probable validity of assumptions and is used below in estimating length of the calving interval.

The basic data used for estimating average length of calving interval were the relative frequencies of adult females in several reproductive conditions (Table 8). Adult females were defined as those with at least one corpus luteum or corpus albicans. Senile females were those with 10 or more corpora albicantia, no corpus luteum or Type 1 or 2 corpora albicantia and ovaries weighing less than 3.5 g. Resting/estrus females were those nonsenile adults that were neither pregnant nor lactating. Many of these (16 to 31%) had a corpus luteum. The corpus luteum may have represented an undetected very early pregnancy, a very recently aborted pregnancy, loss of a calf shortly after birth (resulting in cessation of lactation), or may have been a corpus luteum of ovulation. All of these alternatives may be represented in the samples.

In calculating the proportions of females in the three phases of pregnant, lactating, and resting (Table 9), senile females were excluded. One-half of the animals simultaneously pregnant and lactating were assigned to the pregnant category and one-half to the lactating category.

The average length of calving interval was estimated by two methods — 1) using the estimates of gestation and lactation periods and 2) using the percentage of females pregnant. The data for the 3 yr are comparable (Table 9), with the exception of possible existence of a trend in proportion resting; therefore, length of calving interval was estimated from the pooled data. Eighty-four and one-half percent of reproductive females were pregnant or lactating. Pregnancy (11.5 mo) plus lactation (11.2 mo) total 22.7 mo. If the proportion in a phase is equal to the proportion of the total

TABLE 8.—Reproductive condition of 1,114 adult female specimens of *Stenella attenuata*, collected 1973.[1]

	1971		1972		1973		Total	
	No.	%	No.	%	No.	%	No.	%
Pregnant only (P)	31	36.0	180	39.7	233	40.7	444	39.6
Lactating only (L)	29	33.7	180	39.7	223	38.9	432	38.8
Pregnant and lactating (PL)	13	15.1	16	3.5	17	3.0	46	4.1
Resting/estrus (R)	11 $\left(\frac{A}{B}\right)$ $\left(\frac{3}{8}\right)$	12.8	64 $\left(\frac{10}{54}\right)$	14.1	94 $\left(\frac{29}{65}\right)$	16.4	169 $\left(\frac{42}{127}\right)$	15.2
Senile[2]	2	2.3	15	3.3	6	1.0	23	2.1
Total	86	100	455	100	573	100	1,114	100

[1]In the resting/estrus category, subcategories A and B (in parentheses) are specimens with and without a corpus luteum, respectively.
[2]≥10 corpora, no Type 1 or 2 corpora, and ovaries ≤3.5 g.

TABLE 9.—Proportions of 1,091 adult reproductive females of *Stenella attenuata* in pregnant, lactating, and resting/estrus phases.

	1971		1972		1973		Total	
	No.	%	No.	%	No.	%	No.	%
Pregnant (P + ½PL in Table 8)	37.5	44.6	188	42.8	241.5	42.6	467	42.8
Lactating (L + ½PL)	35.5	42.3	188	42.8	231.5	40.8	455	41.7
"Resting" (R)	11	13.1	64	14.4	94	16.6	169	15.5
Total reproductive females	84	100	440	100	567	100	1,091	100

calving interval spent in that phase, then total length of the interval cycle is 22.7 mo divided by 0.845, or 26.9 mo.

A second estimate was obtained directly from the proportion of females pregnant. In calculating this proportion, all pregnant animals were included (P + PL in Table 8): 490 of 1,091 reproductive females were pregnant, or 44.9%. Division by length of pregnancy, 0.958 yr (11.5 mo), yields an estimate of annual pregnancy rate, 0.469. The reciprocal of pregnancy rate, 2.133 yr, or 25.6 mo, is an estimate of average length of calving interval.

Both estimates of length of calving interval, 26.9 and 25.6 mo, are overestimates to the extent that the "resting" females with corpora lutea represented uncounted pregnancies, but the effect can be at most very minor. For example, if all these females represented undetected pregnancies or pregnancies aborted during capture, the unlikely extreme case, the estimates would be 25.7 and 24.7 mo respectively, an average difference of about 1 mo. Since the "resting" females with corpora lutea probably represent a mixture of causes and conditions, including nonfertile ovulations, the probable effect on the estimates is less than 1 mo. Considering this factor and the closeness of the two estimates to each other, it seems certain that the true length of the interval is between 24 and 27 mo. The lower of the two estimates, which is based on fewer assumptions and calculations, was rounded off to 26 mo and is used below in further analysis of life history. The average pattern of events then, consists of 11.5 mo of pregnancy, 11.2 mo of lactation, and 3.3 mo of resting and/or estrus.

Overlapping Lactation and Pregnancy

About 9.6% of lactating females were also pregnant (Table 8). Most had fetuses less than 35 to 40 cm long (Figure 26), about halfway through the gestation period. This suggests that overlap when it occurs is usually about 5 to 6 mo long, i.e., conception occurs about halfway through the lactation period of about 11 mo, making the calving interval about 20 mo long instead of 26. The very few lactating females with near-term fetuses may have conceived during postpartum estrus or may have begun to lactate shortly before parturition.

The data on Graafian follicles are consistent with the theory that postpartum estrus occurs during lactation (Figure 34). The largest follicle in the ovaries of resting/estrus females (including those presumably about to ovulate) is on the average 3 to 4 mm in diameter. After ovulation and conception, the remaining large follicles regress rapidly to about 2 mm (or become lutealized or atretic). There is a further net decline during gestation to about 1.5 mm, and during lactation the main modal diameter is about 1.0 mm. During both pregnancy and lactation, however, about 10% of the females (excluding senile individuals, as defined above) have follicles that are within the size range (≥3.0 mm) of the presumably ripe follicles present during the resting/estrus phase. This is most clear-cut during lactation. Most of the larger follicles during pregnancy occur in females having fetuses 400 to 500 mm long, or about halfway through the gestation period (Figure 34).

Decrease in Reproductive Rate with Age

Reproductive rate decreases with age. Age-specific estimates of pregnancy rates and lactation rate were calculated from a random sample of the data for specimens for which teeth were sectioned (stratified to insure representation of corpora-number strata in about the proportions as in the entire sample). The analysis shows decline of pregnancy rate from about 0.6 at 8 to 9 layers to about 0.3 at 16 to 17 layers (Figure 35). The weighted rate for the pooled sample of 138 used in the calculation was 0.51, comparable to the rate of 0.47 obtained for 1,091 animals (above). The specimens for which teeth were sectioned were about one-third from 1971 and two-thirds from 1972, with a few specimens from earlier years. Lactation rate

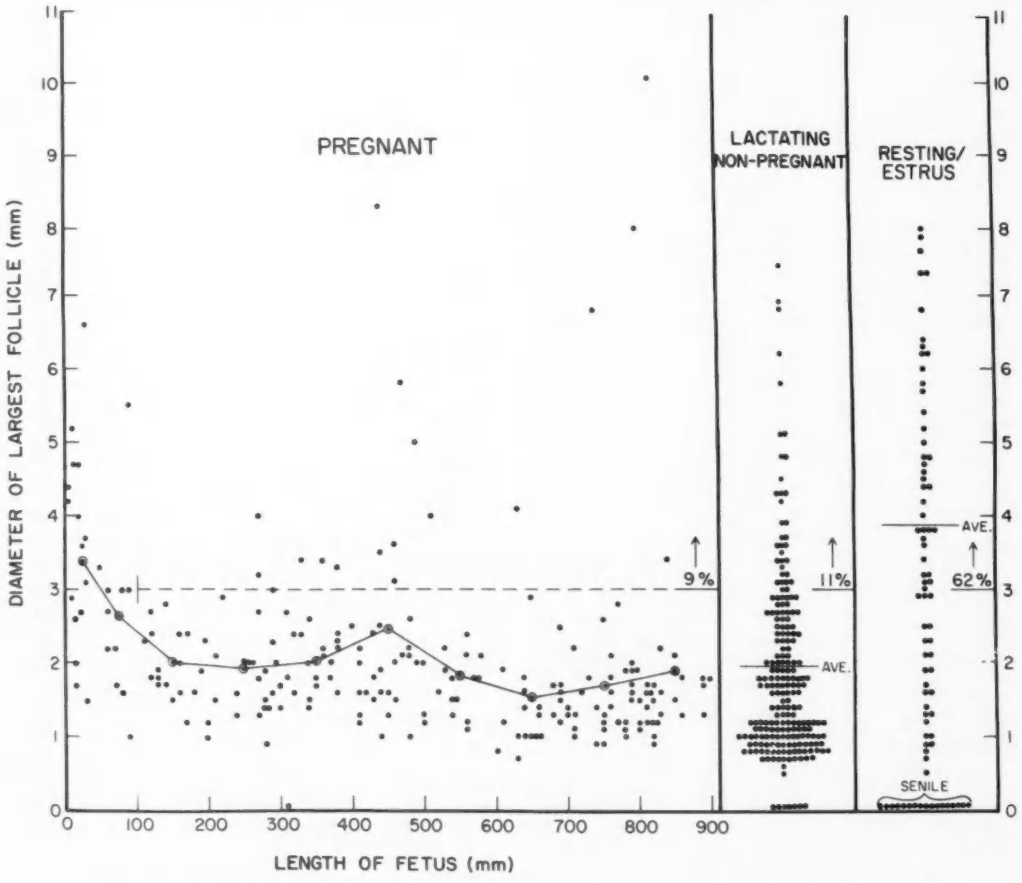

FIGURE 34.—Diameter of largest follicle in pregnant, lactating, and resting females of *Stenella attenuata*.

(Figure 35) increases from about 0.1 at 8 layers to about 0.6 at 12 layers and then again decreases to about 0.5.

The initial very low lactation rate compared to pregnancy rate, of course, reflects the fact that a very high percentage of the young females are pregnant for the first time and thus cannot be lactating. The lactation rate climbs rapidly to a level about equal to the pregnancy rate (at about 12 layers) and behaves like the pregnancy rate thereafter. The apparent decline of reproductive rates in older females may be related to the physiological or social mechanisms that cause the appearance of postreproductive females in this age group (see above; not included here).

Sex Ratios

The overall sex ratio was 44.9% males and 55.1% females (Figure 36). Many large samples examined were predominantly female. Fourteen of 32 single-school samples of 50 or more specimens were more than 60% female, whereas none was more than 60% male. The largest single-school sample examined (342) was almost half and half males and females.

Sex ratio changes with age (Table 10). This is, of course, making the assumption that the samples examined were representative of the population. Neonates and two-tone animals were almost equally divided between the sexes, but only about

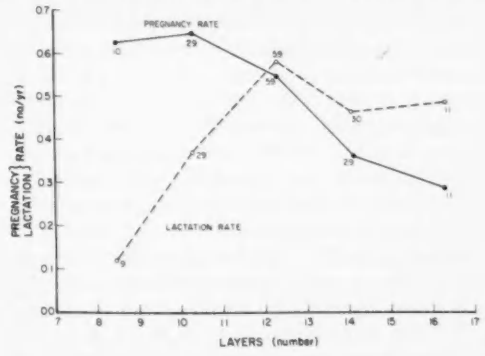

FIGURE 35.—Age-related changes in pregnancy (solid line) and lactation rates (dashed line) in *Stenella attenuata*, based on tooth layer data. Postreproductive females not included.

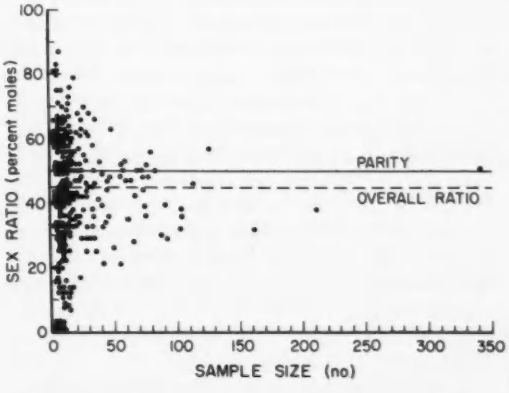

FIGURE 36.—Scatterplot of sex ratio (percent males) on sample size in single-school samples of five or more specimens of *Stenella attenuata*. Overall ratio (dashed line) from Table 12.

TABLE 10.—Sex ratio, by color pattern stage, in 9,371 specimens of *Stenella attenuata*, 1971-73.

Color pattern stage	Males		Females		
	No.	%	No.	%	Total
Neonate	205	49.8	207	50.2	412
Two-tone	666	48.7	701	51.3	1,367
Speckled	609	47.8	666	52.2	1,275
Mottled	569	43.8	729	56.2	1,298
Fused	2,154	42.9	2,865	57.1	5,019
Total	4,203	44.9	5,168	55.1	9,371

43% of the adults examined were males. The greatest change in ratio, from 48.0 to 43.5% male, comes about during the transition to mottled coloration between 7 and 8 layers of age. Assuming random sampling of the population, male and female mortality rates must diverge sharply at this point.

Gross Annual Production

An estimate of average gross annual production of calves for 1971 to 1973 was calculated based on the estimate of annual pregnancy rate, the color pattern phase data, and the proportions of mottled and fused females found to be sexually mature (Table 11).

Seven hundred and twenty-nine of 9,371 animals were mottled females (7.8%) and 2,865 were fused females (30.6%). Of 127 mottled and 1,141 fused females, 47.4 and 88.4% were sexually mature, respectively (Table 11). Average pregnancy rate was 0.469. Production = $[(0.078 \times 0.474) + (0.306 \times 0.884)]0.469 = 0.144$ of the population per year.

TABLE 11.—Sexual maturity (presence of ovarian corpora) in mottled and fused females of *Stenella attenuata*, 1971-73.

Year	Mottled			Fused		
	N	Mature		N	Mature	
		No.	%		No.	%
1971	6	5	(—)	99	82	(82.8)
1972	92	37	(40.2)	473	417	(88.2)
1973	170	85	(50.0)	569	510	(89.6)
Total	268	127	(47.4)	1,141	1,009	(88.4)

Schooling in Relation to Reproduction

Kasuya (1972) reported changes in structure and size of schools of *S. coeruleoalba* correlated with breeding condition and breeding activities. Kasuya et al. (1974) proposed a complex hypothetical system of school formation and breakdown determined by reproductive activities in the Japanese population of *S. attenuata*. They suggested that juveniles of *S. attenuata* in Japanese waters leave breeding schools and school separately, rejoining the breeding schools at puberty. There is nothing to indicate that this happens in the eastern Pacific. We examined the coloration structure (= age structure) of single-school samples. Of 324 single-school samples of seven or more animals, only 1 (of 17 animals) contained no adults (or neonatal calves, which would indicate presence of adult lactating females in the school). This sample (8 two-tone, 2 speckled, and 7 mottled) was from a school of about 600 spotted porpoise, *S. attenuata*, congregated with about 600 spinner porpoise, *S. longirostris*. Given that about half the animals examined were adults, the probability of

a single-school sample of seven containing no "fused" individuals is about 0.01 ($= 0.5^7$). If schools consisting only of juveniles were common, many more all-juvenile samples would have been encountered. Conversely, juveniles (two-tone, speckled, and/or mottled) occurred in all but 3 of the 324 samples. It must be concluded that juveniles probably do not school separately in the eastern Pacific. Another possibility, albeit unlikely, is that all-juvenile schools exist but are not captured by tuna seiners.

COMPARISON WITH THE JAPANESE POPULATION

Many of the estimates of life history parameters presented here differ from those published by Kasuya et al. (1974) for the relatively unexploited population of *S. attenuata* in Japanese waters (Table 12). The differences could be caused by 1) differential procedures or analytical methods, 2) intrinsic racial differences between the populations, or 3) differential population status, e.g., exploited versus unexploited. The comparisons below of similarly calculated average estimates, of course, rest on the assumption that the overall samples in both cases were not biased with respect to age or sex. The major sampling differences between the two studies is that the Japanese sample consisted mostly of large samples from a few schools, whereas our sample consisted mainly of aggregated, small samples from many schools. Both studies assume no sampling bias. Comparison of large, single-month samples in the present study with large, single-school samples in the Japanese study (e.g., the October 1972 sample in Figures 15 and 16 with sample number 2 in Figure 2 of Kasuya et al. 1974) indicate very similar length-frequency distributions and support the idea that the aggregated samples are probably not biased, or, if biased, are biased in the same way. This inference is, of course, based on the assumption that the underlying population structures are about the same in the two populations.

The estimate of Kasuya et al. (1974) of length at birth was based on only 5 full-term fetuses and newborn calves versus 86 in the present study. Our estimate can, therefore, be considered more reliable, although the possibility does exist that length at birth is greater in the Japanese population. The difference between the estimated lengths at 1 yr for the two populations is about the same as the difference between the estimates of length at birth. Estimated length at attainment of sexual maturity and maximum length (for males) are also greater for the Japanese samples. The estimate of length at maturity of males is greater in spite of the fact that Kasuya et al. used a lower testis-weight criterion than we did (68 versus 100 g). The average lengths of both adult males and

TABLE 12.—Comparison of estimates of average life history parameters of *Stenella attenuata* by Kasuya et al. (1974) and in present paper.

Parameter (average)	Kasuya et al.	Perrin et al.
1. Length at birth	89 cm	82.5 cm
2. Growth rate in 1st year	4.5 cm per mo	4.6 cm per mo
3. Length at 1 yr	143 cm	138 cm
4. Length at onset of sexual maturity:		
Males	197 cm	~195 cm
Females	187 cm	181 ± 1 cm
5. Age at onset of sexual maturity:		
Males	10.3 layers (10.3 yr)	12 layers (6-11 yr)
Females	8.2 layers (8.2 yr)	9 layers (4.5-8 yr)
6. Average length of sexually mature adults:		
Males	204-207 cm	200.7 cm
Females	192-195 cm	187.3 cm
7. Maximum length:		
Males	234 cm	226 cm
Females	220 cm	220 cm
8. Maximum number of consistently readable tooth layers	~13	12-13
9. Average ovulation rate (based on layers)	0.8 per layer (0.8 per yr)	~1 per layer (1 or 2 per yr) in fully mature, more in younger
10. Pregnancy rate (overall)	0.27 per yr	0.47 per yr
11. Breeding seasons	3 per yr	multiple
12. Gestation	11.2 mo	11.5 ± 0.2 mo
13. Lactation	29.3 mo	11.2 mo
14. Resting	9.8 mo	3.3 mo
15. Length of calving interval	4.19 yr	2.17 yr
16. Sex ratio:		
Overall	0.76 male:1 female	0.81 male:1 female
At birth	1.3-1.5:1	1.00:1
Adults	0.58:1	0.75:1

females are also greater in the Japanese population, and in this case, all four of the estimates are based on large and certainly adequate samples. These differences all suggest that the Japanese form is about 6 to 8 cm larger than the eastern Pacific form.

The estimates of Kasuya et al. (1974) of age at attainment of sexual maturity are based on their conclusion that one tooth layer corresponds to 1 yr of growth. It appears from comparisons of their first-year growth curve with ours (note rate in first year and length at 1 yr) that our first two layers correspond to their first layer. Kasuya (1972) in his paper on growth of *S. coeruleoalba* mentioned observing "one or two faint translucent layers in the thick opaque layer accumulated just after the birth" that were "not used for age determination because it was not expected to show the annual accumulation cycle," and Kasuya et al. (1974) stated that the "dentinal growth layers of this species [*S. attenuata*] does not differ so much from that of *S. coeruleoalba*." After the first year, our hypothesis 2 corresponds to the assumption of Kasuya et al. of one layer per year, e.g., nine layers of Perrin et al. (1973) = eight layers of Kasuya et al. = 8 yr.

The average length of calving interval in both studies was estimated by several methods that converged on the respective central estimates. One minor difference between the two analyses is that Kasuya et al. (1974) did not exclude postreproductive females from the "resting/estrus" group. Thus, their estimate of the average resting/estrus period of 9.8 mo may be a slight overestimate. The probable effect of this on the estimate of length of total calving interval is very small, however, and it therefore seems that the estimates are analytically comparable and that the difference between them is real. Kasuya et al. estimated that individual intervals in the Japanese population vary from 23 to 60 mo, with modes at 28 to 30, 36 to 38, and 54 to 56 mo. The potential thus probably exists for a shift in average length from 50 mo (4.17 yr) to 26 mo (2.17 yr) under exploitation.

Kasuya et al. (1974) used the same methods used here to estimate length of the lactation period and arrived at a "best" estimate of 29.3 mo, some 18 mo longer than our estimate of 11.2 mo. They found that the major shift from milk to solid food occurs at body length of about 133 cm, about the same as in our sample, but that some suckling and lactation of the mother continues for an average additional 20 mo. The prolonged suckling is probably nutritionally a largely nonfunctional aspect of general prolonged parental care. It has been suggested on the basis of comparison of the life histories and behavior of mysticetes and odontocetes that this period in odontocetes may allow for "sophisticated" communicational-navigational training (Brodie 1969). Thus the apparent shorter lactation period in the eastern Pacific, and the concomitant shorter calving interval and higher pregnancy rate, does not necessarily mean earlier effective weaning, but may reflect a truncated parental care period.

The apparent overall sex ratios are almost the same for the two populations, but the proportion of males was higher at birth and lower at maturity in the Japanese samples than in the eastern Pacific samples. A lower proportion of males at birth could be a response to exploitation. Kasuya et al. (1974) suggested that the very low proportions of males in mature age-classes in the Japanese catches could be partially caused by segregation of adult males or by differential catchability but are largely due to differential mortality rates. If the decrease in proportion of males with age is caused by differential mortality, the apparent faster decrease in the Japanese population must mean that the disparity in mortality rates between the sexes is greater there than in the eastern Pacific.

In summary, the two sets of estimates differ in a consistent way, and the differences are real. It seems possible that the differences in some way reflect exploitation in the eastern Pacific.

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GROWTH OF LABORATORY-REARED NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, FROM SOUTHERN CALIFORNIA

GARY T. SAKAGAWA AND MAKOTO KIMURA[1]

ABSTRACT

The northern anchovy, *Engraulis mordax*, was experimentally reared in the laboratory at the Southwest Fisheries Center, La Jolla, Calif. Data from three experiments were used to empirically fit a two-phase Gompertz growth model. The model describes growth from hatching to about 20 mo of age. It was estimated that the average length of laboratory-reared anchovies is 102 mm at 1 yr old and 119 mm at 2 yr old. Growth of laboratory-reared anchovies was comparable to that of anchovies in the wild.

Attempts to rear the northern anchovy, *Engraulis mordax*, at the Southwest Fisheries Center (SWFC), La Jolla, Calif., were begun in 1966 when G. O. Schumann collected anchovy larvae in the ocean off La Jolla and successfully reared them using wild plankton as food in the laboratory (Bardach 1968). Schumann's success was followed by other laboratory experiments in which anchovies were reared from eggs, larvae, and juveniles that were caught in the ocean (Table 1). In 1970, Leong (1971) developed a method for artificially inducing anchovies to spawn by controlling the photoperiod and injecting hormones. This technique is currently used at the SWFC to produce eggs and to rear anchovies for experimental purposes.

One of the purposes of the rearing experiments at the SWFC has been to obtain physiological and biochemical information needed for describing the energy budget of the northern anchovy, and to relate the results to the feeding dynamics of the anchovy population in the California Current, which consists of primarily young fish less than 3 yr old. Growth data are needed for analysis of the budget, and various attempts have been made to measure growth in the laboratory. Kramer and Zweifel (1970) and Lasker et al. (1970) reported growth rates of anchovy larvae. In this report we extend their analyses to include growth from hatching to about 20 mo old. We also present a mathematical model that describes this growth and compare our results with those of other investigators.

SOURCES OF DATA

Data primarily from experiments of G. O. Schumann (Schumann-I; Schumann-II), G. O. Schumann and A. Saraspe (Schumann-III), and R. Leong (pers. commun., SWFC) were used in our study (Table 1).

Schumann-II successfully reared larval anchovies for 22 days at about 22°C water temperature, which is higher than the temperature (15° to 16°C) at which anchovy larvae are frequently found in large numbers in the California Current (pers. commun., P. Smith, SWFC). The larvae were fed wild plankton and samples were taken for length measurement approximately daily.

Schumann-III reared anchovies from the egg stage through the juvenile stage in aquaria for 83 days on a diet of wild plankton, *Artemia salina*, and commercial trout food. The experiment was conducted from March to June and the water temperatures in the aquaria were not recorded. However, during March to June the average water temperature in rearing aquaria at the SWFC is generally about 18° to 22°C.

Leong (pers. commun.) obtained juvenile anchovies from a live-bait dealer and reared the fish to maturity in a 4.6-m diameter pool (13.2 kl) with circulating seawater. The water temperature in the pool was a few degrees higher than the prevailing water temperature off Scripps Pier, La Jolla, site of the water intake for the experimental pool (Lasker and Vlymen 1969). Leong fed the fish a diet of *Artemia salina*, ground squid and anchovies, and commercial trout food. Once a month about 25 fish were sacrificed for length and weight measurements.

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TABLE 1. — Laboratory experiments of rearing the northern anchovy at the Southwest Fisheries Center, La Jolla, Calif.

Source	Life stage at start	Start of rearing	Rearing duration (days)	Average length (mm)		Food
				Start	Finish	
Hunter (1976)	Eggs	April	74	4.0	35.0	*Gymnodinium splendens*, *Brachionus plicatilis*, *Tisbe furcata*, and *Artemia salina*
Kramer and Zweifel (1970)	Eggs	August and September	35	3.2	17.4	Wild plankton and *A. salina*
Lasker et al. (1970)	Eggs	February	50	3.4	21.0	*Bulla gouldiana*, *G. splendens*, and *A. salina*
Leong (unpubl. data)[1]	Juveniles	April	474	88.3	117.7	Squid, anchovy, *A. salina*, and trout food
Paloma (see text footnote 3)	Juveniles	November	624	75.0	106.2	*Artemia salina* and trout food
Schumann-I (G. O. Schumann unpubl. data)[2]	Larvae	March	97	18.0	81.9	Wild plankton
Schumann-II (Kramer and Zweifel 1970)	Eggs	March	22	2.9	16.2	Wild plankton
Schumann-III (G. O. Schumann and A. Saraspe unpubl. data)[2]	Eggs	March	83	3.5	67.1	Wild plankton, *A. salina*, and trout food
Theilacker and McMaster (1971)	Eggs	—	19	—	12.0	*Gymnodinium splendens*, *B. plicatilis*, and *A. salina*

[1]Pers. commun., Southwest Fisheries Center, La Jolla, Calif.
[2]Data are on file at the Southwest Fisheries Center, La Jolla, Calif.

In all of these experiments the fish were from the southern California stock (Vrooman and Smith 1971), reared at laboratory ambient water temperature, and not subjected to experimental treatment or excessive handling. All fish sampled for measurements were sacrificed. The length measurement is standard length.

TREATMENT OF DATA

The age of anchovies reared by Schumann-II and Schumann-III were known because the anchovies were hatched from eggs at the start of the rearing experiments. In Leong's (pers. commun.) experiment, the exact age of his fish was not known because juvenile fish of average length of 88.3 mm were used at the start of the experiment. We estimated the age of Leong's fish from data from Schumann-I in which anchovies were reared for 97 days from an average length of 18.0 to 81.9 mm (Table 1), and data from Schumann-III which indicated that an 18.0 mm fish, raised from eggs, was about 30 days old. Our age estimate is 4 mo.

Several mathematical models describing growth of organisms are available (e.g., Parker and Larkin 1959; Richards 1959; Laird 1969). The commonly used models in fisheries are the exponential, the von Bertalanffy, and the Gompertz models (Beverton and Holt 1957; Silliman 1969). The Gompertz model was selected for our study because it was shown by Kramer and Zweifel (1970) to be better than the exponential model for describing growth of laboratory-reared anchovy larvae and because it generally describes the growth of fishes fairly well. Also, preliminary analysis of our data indicated that the von Bertalanffy model poorly described the growth of young fish.

The Laird version of the Gompertz growth model (Laird 1969) describes an asymmetric sigmoid curve of the form.

$$L_t = L_0 \exp \{C \left[1 - \exp (-at)\right]\}$$

where L_0 = length at zero age or hatching
C = a constant
a = rate of decay of exponential growth
t = age in months.

This model was fitted to our data using an iterative least squares procedure (Conway et al. 1970). Our goal was to describe growth on a coarse time scale, i.e., monthly rather than on a fine time scale, i.e., daily.

GROWTH FROM HATCHING TO JUVENILE STAGE

The Gompertz growth model and an exponential growth model were applied to data of Schumann-II by Kramer and Zweifel (1970). Both models described the data from Schumann-II reasonably well, although the Gompertz model de-

scribed the data better. In the Kramer-Zweifel analysis the length at zero age, L_0, was fixed at 2.5 mm, the average size at hatching. We also applied the Gompertz growth model to data of Schumann-II. Kramer and Zweifel (1970) used data only for 17 days of growth. We used all of the data of Schumann-II, which included sampling through 22 days of growth, and fitted the model first with L_0 fixed at 2.5 mm and again without this constraint, i.e., L_0 was estimated. The results (Figure 1) indicate that there is not much difference in the curves with L_0 fixed or estimated within the range of the data. Outside the range of the data, the curves diverge considerably and there is a substantial difference; the curve with L_0 estimated has a lower asymptotic length (61 mm) than the curve with L_0 fixed at 2.5 mm (asymptotic length of about 696 mm).

Zweifel and Lasker[2] showed that a two-phase Gompertz curve described the data from Schumann-II better than a single-phase Gompertz curve. The separation of the phases occurred at about 6 days of age, the onset of feeding in anchovy larvae.

Schumann-III reared anchovies for a longer period than Schumann-II. Fish reared by Schumann-II, however, were larger than those reared by Schumann-III at similar ages. For example, at 0.5 mo of age fish reared by Schumann-II averaged 12.1 mm long and fish reared by Schumann-III, 8.2 mm long. Although the sample size is small, this difference is statistically significant at the 1% probability level. Differences in rearing procedures, i.e., diet and temperature of water, probably produced the difference in growth (Kramer and Zweifel 1970; Lasker et al. 1970).

The Gompertz growth model was applied to data from Schumann-III first with L_0 fixed at 2.5 mm and then with L_0 estimated (Figure 2). As in the case with data from Schumann-II, this model describes the growth data reasonably well, and the curve with L_0 estimated has a lower asymptotic length (81 mm) than the curve with L_0 fixed (asymptotic length of about 93 mm).

GROWTH DURING JUVENILE TO ADULT STAGE

Anchovies reared by Leong (pers. commun.) were juveniles at the start of the experiment and grew to an average size of 117.7 mm in 474 days (Table 2). Growth was in steplike stages characterized by rapid growth followed by a leveling off. The first stage was between 4 and 12 mo of age and the second was between 12 and about 20 mo of age.

[2]Zweifel, J. R. and R. Lasker. 1974. Prenatal and postnatal growth of fishes — a general model. Unpubl. manuscr. Southwest Fisheries Center, La Jolla, CA 92038.

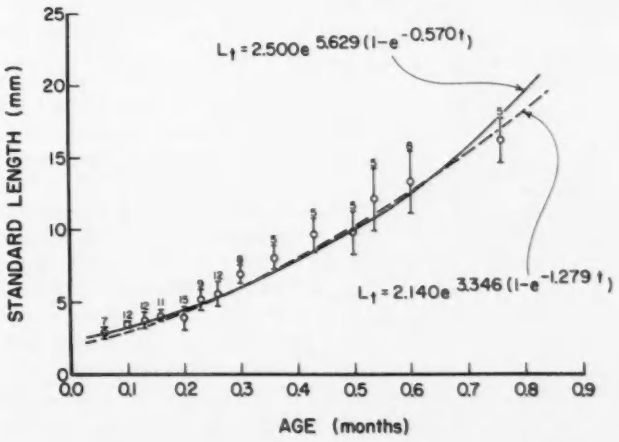

FIGURE 1.—Growth of anchovy larvae reared in the laboratory. The Gompertz growth model of the form, $L_t = L_0 \exp\{C[1 - \exp(-\alpha t)]\}$ is used to describe the data. Solid line is based on L_0 fixed at 2.500 mm and broken line is based on L_0 estimated, 2.140 mm. Data from Schumann-II (Kramer and Zweifel 1970). The mean (circle), one standard deviation on each side of the mean, and sample size are shown.

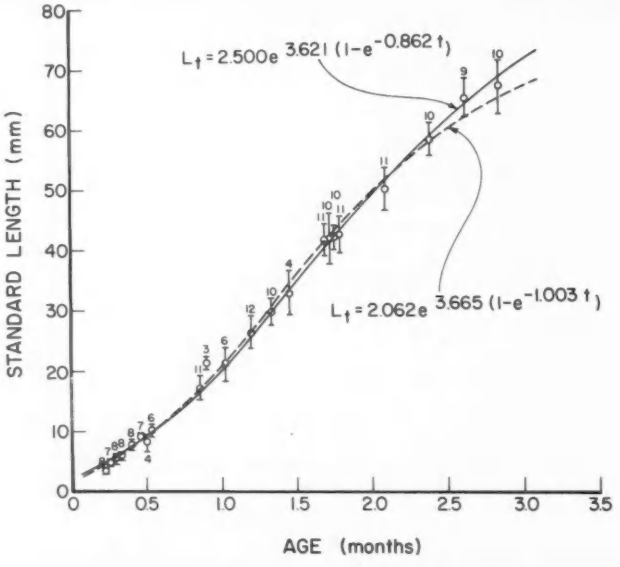

FIGURE 2.—Growth of anchovy reared in the laboratory. The Gompertz growth model of the form $L_t = L_0 \exp\{C[1 - \exp(-at)]\}$ is used to describe the data. Solid line is based on L_0 fixed at 2.500 mm, and broken line is based on L_0 estimated, 2.062 mm. Data from Schumann-III (unpubl. data, Southwest Fisheries Center, La Jolla, Calif.). The mean (circle), one standard deviation on each side of the mean, and sample size are shown.

TABLE 2.—Estimated age and average standard length of northern anchovies reared in the laboratory by R. Leong (pers. commun., Southwest Fisheries Center, La Jolla, Calif.)

Age		Number of fish	Average length (mm)	Standard deviation
Days	Months			
120	4.00	10	88.30	6.34
153	5.10	23	92.35	4.90
189	6.30	24	94.63	5.85
231	7.70	25	97.68	6.40
270	9.00	25	96.48	6.19
301	10.03	23	99.30	5.14
351	11.70	25	101.52	4.59
385	12.83	25	105.72	5.26
413	13.77	25	109.16	5.75
444	14.80	26	109.23	6.07
471	15.70	26	110.58	6.82
503	16.77	25	114.56	6.57
533	17.77	24	117.38	6.11
562	18.73	25	116.32	7.07
594	19.80	25	117.68	6.69

The Gompertz growth model was applied, but did not adequately fit the data. This is characteristic of asymptotic models like the Gompertz model when all the data points are for a segment of the growth curve where growth is relatively slow and the plot of the data exhibits little curvature.

GROWTH FROM HATCHING TO ADULT STAGE

Growth Curve

As indicated earlier, anchovies reared by Shumann-III grew slightly faster than those of Schumann-II, probably due to slight differences in the rearing environment and procedures. Because our goal was to construct a general growth curve and the differences in the data were relatively slight, we elected to disregard the difference and pooled the data from the three experiments (Schumann-II, Schumann-III, and Leong). The Gompertz growth model was applied to the pooled data. The results (Figure 3) indicate that the model does not adequately describe the data. For example, the model overestimates the sizes of fish at about 4 to 12 mo old and underestimates the sizes of fish older than about 13 mo. These biases are caused by the steplike growth pattern which produces plateaus at about 6 mo and 19 mo of age.

To account for this steplike growth pattern, a

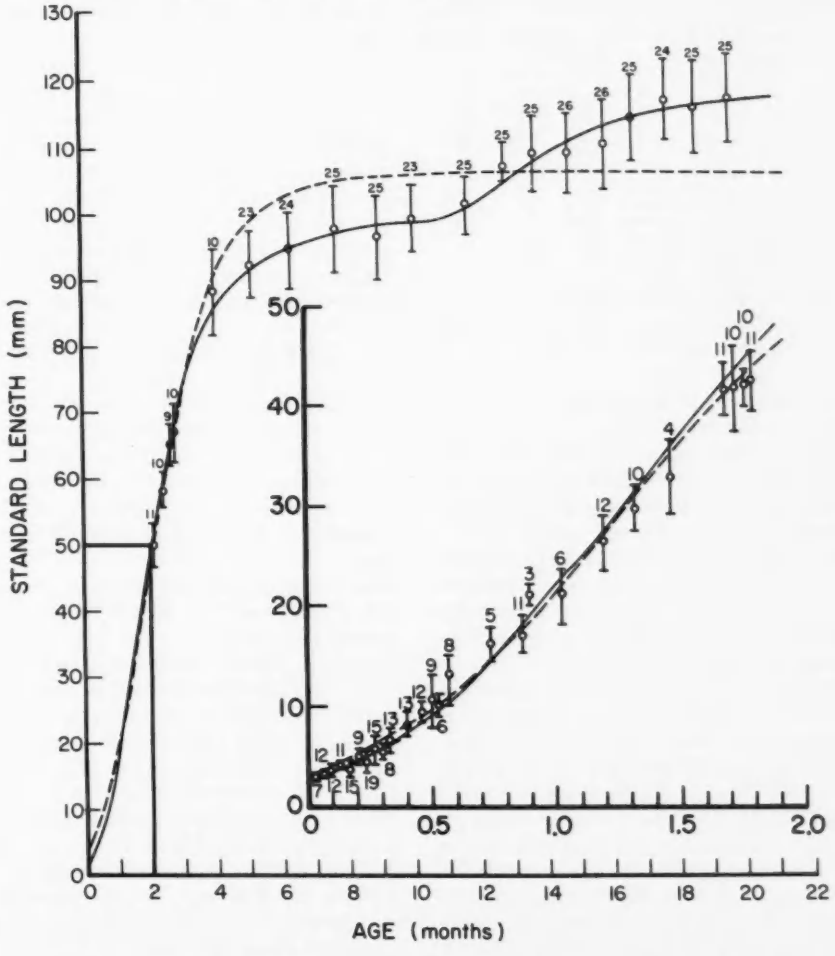

FIGURE 3.—Growth of northern anchovy reared in the laboratory. One-phase (broken line) and two-phase (solid line) Gompertz growth models are used to describe the data. Data from Schumann-II (Kramer and Zweifel 1970), Schumann-III, and Leong (unpubl. data, Southwest Fisheries Center, La Jolla, Calif.). The mean (circle), one standard deviation on each side of the mean, and sample size are shown. Broken line is described by $L_t = 2.825 \exp\{3.623[1 - \exp(-2.877t)]\}$ and solid line by $L_t = 2.745 \exp\{3.563[1 - \exp(-0.848t)]\}$ for $t \leq 11$ mo, and $L_{(t-11)} = 96.782 \exp\{0.213[1 - \exp(-0.258\{t - 11\})]\}$ for $t > 11$ mo.

two-phase Gompertz model (Zweifel and Lasker see footnote 2) was fitted to the data. The two-phase model is essentially two separate Gompertz equations that describe different segments of the growth curve. The equations were fitted simultaneously and the convergence point of the equations was determined on the basis of least squares analysis. Our best fit of the data was with the equation, $L_t = 2.745 \exp\{3.563[1 - \exp(-0.848t)]\}$ for growth from hatching to 11 mo of age and the equation, $L_{(t-11)} = 96.782 \exp\{0.213[1 - \exp(-0.258\{t - 11\})]\}$ for growth from 11 to 20 mo of age (Figure 3). From the equations, the estimated average length of anchovies after 1 yr of life is 101.6 mm and after 2 yr of life, 118.9 mm (Table 3).

TABLE 3.—Estimated growth for the first 24 mo of life of the northern anchovy reared in the laboratory. Estimates are based on a two-phase Gompertz growth curve (see text).

Age (mo)	Standard length (mm)	Age (mo)	Standard length (mm)
hatching	2.7	13	105.5
1	21.0	14	108.6
2	50.4	15	111.0
3	73.2	16	112.9
4	85.9	17	114.5
5	92.0	18	115.6
6	94.7	19	116.6
7	95.9	20	117.3
8	96.4	21	117.8
9	96.6	22	118.3
10	96.7	23	118.6
11	96.8	24	118.9
12	101.6		

General Remarks

The steplike growth pattern is commonly found in fishes. Gerking (1967) reviewed the literature on this subject and noted that many temperate species have seasonal, sigmoid growth curves. Lockwood (1974) recognized this feature in the growth of plaice and brown trout and applied a multiphase von Bertalanffy growth model to describe the data mathematically. His results were satisfactory but because the von Bertalanffy growth equation does not describe a sigmoid curve, his analysis was confined to growth for part of the season only.

In this study we used the Gompertz growth equation to describe the sigmoid curve. The two-phase model satisfactorily described our data for laboratory-reared anchovy, and a cycle that occurs at 12-mo intervals is evident in our results. This is quite similar to the seasonal growth patterns described by Gerking (1967), Mann (1971), Kroger et al. (1974), and others. The cycle indicates that for the northern anchovy, about 95% of the first year's growth is completed by the 8th month of life and about 91% of the second year's growth is completed by the 20th month of life.

If this cyclic pattern in growth also occurs in anchovies in the wild, then it may have a considerable impact on yield models, such as yield-per-recruit models, and on management decisions. It might be that the best harvesting strategy in terms of maximum yield-per-recruit is during the period of the cycle when growth is relatively slow, i.e., period of plateau. It seems important, therefore, that a multiphase growth function be considered for use in yield models for northern anchovy.

We point out the possibility that the cyclic pattern could have been artificially created because our data were from three cohorts that were reared under different laboratory conditions during different periods of the year and the ages of fish reared by Leong (pers. commun.) were estimated. However, we discount that possibility because the cyclic pattern persists even if our age estimates of Leong's fish were off by 1 or 2 mo. Rearing conditions, on the other hand, could have produced the cyclic pattern if the pattern is influenced primarily by environmental factors, e.g., temperature, length of day, and food density and quality.

WEIGHT-LENGTH RELATION

Weight-length relations for the northern anchovy were reported by several investigators (Table 4). Only Lasker et al. (1970), however, reported on estimates for laboratory-reared anchovies, and their estimates were for anchovy larvae.

Length and weight data were collected by Leong (pers. commun.) and Paloma[3] from fish reared in their experiments. We used their data from 757 fish to estimate the weight-length relation of laboratory-reared anchovies of 70 to 131 mm long. Data from Paloma were only from fish in their first year of life, in which growth was somewhat similar to that of fish reared by Leong. Separate estimates were made for males and females (Table 4), and the results subjected to covariance analysis (with log transformed data) to test whether the relation could be represented by a single line. The analysis indicated that the separate lines were parallel and not significantly different from a common line. The data were, therefore, pooled and a weight-length relation estimated for the combined (all sexes) data (Table 4).

Our estimates are compared with those of Collins (1969) for anchovies from southern California (Figure 4). Collins based his estimates on data from anchovies caught in the reduction fishery off southern California. For a given length, fish examined by Collins were lighter than the laboratory-reared fish. This phenomenon appears common for fishes (Kramer 1969; Kimura and Sakagawa 1972). Kimura and Sakagawa (1972) mentioned that for Pacific sardines, differences in diet and reduced amount of exercise because of confinement were some possible causes for

[3]Paloma, P. 1971. Annulus formation in the scale of marked anchovy *Engraulis mordax* Girard. Unpubl. manuscr. Southwest Fisheries Center, La Jolla, CA 92038.

TABLE 4.—Coefficients of the weight-length relation for the northern anchovy as reported by various investigators. The coefficients are for the equation, weight = $a \times \text{length}^b$.

Origin of sample	Source	Rearing environment: Ocean	Rearing environment: Laboratory	Sex	Number of fish	b	a	Unit of measure: Length	Unit of measure: Weight	Range of length (mm)
Southern California	Clark and Phillips (1952)	X		Combined sexes	(1)	3.453	2.7×10^{-4}	mm	ounce	56-134
	Collins (1969)	X		Male	926	3.049	8.1×10^{-6}	mm	gram	97-161
	Collins (1969)	X		Female	1,513	2.984	1.1×10^{-5}	mm	gram	
	Lasker et al. (1970)		X	Combined sexes	63	3.324	1.5×10^{-4}	mm	mg	3- 25
	Present study[2]		X	Male	257	3.521	1.0×10^{-6}	mm	gram	73-126
	Present study		X	Female	500	3.433	1.5×10^{-6}	mm	gram	70-131
	Present study		X	Combined sexes	757	3.461	1.4×10^{-6}	mm	gram	70-131
Central California	Clark and Phillips (1952)	X		Combined sexes	(1)	3.252	7.2×10^{-6}	mm	ounce	114-160
	Collins (1969)	X		Male	270	2.805	2.7×10^{-5}	mm	gram	80-171
	Collins (1969)	X		Female	407	2.743	3.6×10^{-5}	mm	gram	

[1]Clark and Phillips (1952) used data from 17 samples from southern California and 77 samples from central California but they did not specify the number of fish in each sample.

[2]Unpublished data from R. Leong and P. Paloma (pers. commun.), Southwest Fisheries Center, La Jolla, Calif. The coefficients with the more appropriate functional regression (Ricker 1973) are: 1) male, $a = 7.0 \times 10^{-7}$, $b = 3.606$; 2) female, $a = 1.0 \times 10^{-6}$, $b = 3.518$; 3) combined sexes, $a = 9.2 \times 10^{-7}$, $b = 3.547$.

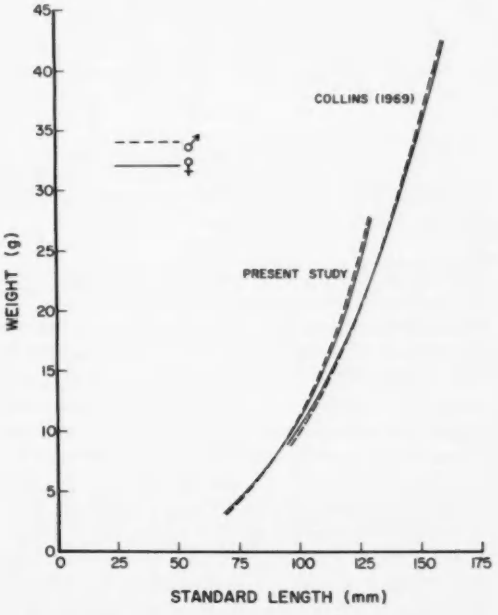

FIGURE 4. — Weight-length relation for northern anchovy from southern California. Laboratory-reared fish were used in present study, and fish caught in the California reduction fishery were used by Collins (1969).

laboratory-reared fish being heavier than fish in the wild. Zweifel and Lasker (see footnote 2) mentioned the possibility that the differences arise when the curves are based on fish in different phases of their growth cycle.

COMPARISONS OF GROWTH

Growth of anchovies reared in the laboratory was studied by Kramer and Zweifel (1970), Lasker et al. (1970), Theilacker and McMaster (1971), Hunter (1976), and Paloma (see footnote 3). Kramer and Zweifel and Lasker et al. studied the effects of diet and water temperature on growth of anchovy larvae. They concluded that larval growth was best at 22°C with wild plankton as a food source. The growth curve of Figure 3 for the larval stage is for fish reared on wild plankton and *Artemia salina* at about 22°C. It is the best so far attained in the laboratory.

Theilacker and McMaster (1971) and Hunter (1976) reared anchovy larvae on cultured foods. Results of their studies show that growth of anchovies on cultured food diets is about the same as that on wild plankton.

Paloma (see footnote 3) obtained juvenile anchovies from a live-bait dealer and reared the fish in the laboratory for 624 days (Table 1). He injected oxytetracycline hydrochloride into the fish at various times to label the body structures for ageing. At 2-wk intervals, scales and data on body measurements were collected. Fish reared by Paloma started at a smaller average size (75 mm long) than fish reared by Leong (pers. commun.) (88 mm long) and grew at a much slower rate (21 mm in about 470 days versus 30 mm in about 470 days for Leong's fish) without a noticeable steplike pattern. Perhaps the frequent handling, injection of tetracycline, and small size of the rearing pool (2.74-m diameter) contributed to the slow growth and eliminated the steplike pattern.

Clark and Phillips (1952), Miller et al. (1955), Collins (1969), and Collins and Spratt (1969), studied growth of anchovies caught in the California fisheries. They used scales and otoliths for ageing fish to the nearest whole year. Clark and Phillips reported their results for the combined

southern and central California fisheries. Miller et al., Collins, and Collins and Spratt, on the other hand, reported their results separately for each fishery.

To compare growth of anchovies in the wild with that of laboratory-reared anchovies, we limited the comparison to fish from southern California to eliminate possible regional biases in growth. We also adjusted Miller et al.'s (1955) data upward by 1 yr to make them comparable to those of Collins (1969) and Collins and Spratt (1969) (Figure 5). This was necessary because Miller et al. did not correct their age readings for date of capture (August to March) and growth on the margin of the scale relative to the birthdate (April 1); hence, they underestimated the age of their fish by approximately 1 yr.

The growth curves in Figure 5 indicate that anchovies in the wild are 95 to 115 mm long at about 1 yr old and 115 to 125 mm long at about 2 yr old and possibly growth was slower in the 1960's than in the 1950's owing to the dramatic increase in the northern anchovy population (Spratt 1975). Our growth estimates for laboratory-reared anchovies are 102 mm for 1 yr olds and 119 mm for 2 yr olds; hence, growth of laboratory-reared fish seems to be similar to that of anchovies in the wild. However, we note that this direct comparison is not entirely valid because inherent biases exist in the growth curves in Figure 5. The biases exist because: 1) larger fish are generally more available to the reduction fishery than the live-bait fishery (Messersmith 1969) and thus are overrepresented in the data for the reduction fishery; 2) live-bait fishermen "consciously avoid taking large anchovies, since they are less desirable for bait than smaller anchovies" (MacCall 1973:5-6) and thus large fish are underrepresented in the data for the live-bait fishery; 3) the true birthdate of anchovies aged by otolith or scale readings is not known although it is known that the birth date varies (Kramer and Smith 1971; Smith 1972), the ages, therefore, are not exact ages; and 4) growth of several year classes are averaged and consequently, variability in growth is reduced.

Spratt (1975), who also studied growth of the northern anchovy from otoliths, accounted for some of these biases by using back-calculated lengths and fish from the reduction fishery, live-bait fishery, and catches of a research vessel. He estimated that the mean standard length of anchovies in the wild is 92 and 112 mm at the end of the first and second year of life, respectively. These

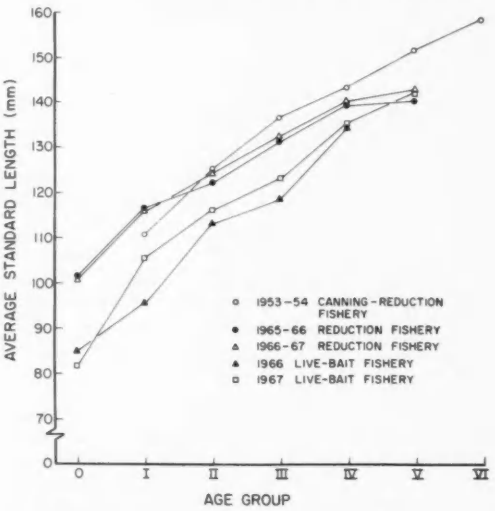

FIGURE 5.—Growth curves for northern anchovy caught off southern California in the fisheries for reduction (Collins 1969), live-bait (Collins and Spratt 1969), and canning-reduction (Miller et al. 1955).

estimates are somewhat less than ours for laboratory-reared fish but they are close.

It appears that growth of anchovies in the wild is similar to that estimated, on an annual basis, from our growth curve. We have not demonstrated, however, whether there is a cyclic pattern in growth of anchovies in the wild similar to that revealed in our results for laboratory-reared fish. On the other hand, studies on growth of other temperate fishes have shown that a seasonal cycle is common, which leads us to believe that a seasonal cycle exists for anchovies in the wild. The use of our growth curve for describing the feeding dynamics of northern anchovies of at least 2 yr of age in the California Current is therefore practical until a seasonal growth curve is described for anchovies in the wild.

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Zweifel read the manuscript and offered valuable comments and suggestions. Robson Collins and members of his staff at the California Department of Fish and Game read the manuscript and brought to our attention related studies that were in press.

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DEVELOPMENT AND USE OF SONAR MAPPING FOR PELAGIC STOCK ASSESSMENT IN THE CALIFORNIA CURRENT AREA[1]

ROGER P. HEWITT, PAUL E. SMITH, AND JOHN C. BROWN[2]

ABSTRACT

A method for pelagic fish stock assessment is presented which utilizes a fixed sonar beam for mapping fish schools. Samples of the two major acoustic properties of fish schools are presented, i.e., acoustically derived horizontal dimensions (representative of school volume) and target strengths (which may be representative of school compaction). Sampling biases and sources of sampling variability in the measurement of these properties are discussed. The results of two experiments, conducted to determine the weight of a fish school as a function of its acoustic characteristics, are presented. In the first experiment, an acoustically transparent trap was used to recreate an aggregation of fish and in the second, commercial fishing boats were chartered to capture whole schools. An automated sonar data acquisition and processing system is described and test results presented. The results of paired automated surveys of the Los Angeles (southern California) Bight are presented and discussed. The paper reports development of the sonar-fish school mapping method first documented by P. E. Smith in 1970.

Field investigations, conducted in cooperation with the Navy and the California Department of Fish and Game, indicate a median school size of 30 m diameter, a mean fish density of 15 kg of fish biomass per square meter of horizontal school area, and a biomass estimate of 1.23 to 2.30 $\times$ 10^6 metric tons for pelagic schooled targets in the Los Angeles Bight.

Fishermen have used hydroacoustic apparatus for locating concentrations of fish for almost as long as practical echo sounding devices have been available, although quantification of the information they provide has been attempted only in recent years. Horizontal echo ranging (sonar) to locate fish schools was first used off the coast of California in 1946 (Smith 1947; Smith and Ahlstrom 1948). The 1950 progress report of the California Cooperative Sardine Research program notes the use of sonar and echo sounders on the RV *Yellowfin* for locating fish schools, and cites the "considerable experimental value" of the acoustic apparatus. A research sonar on the RV *David Starr Jordan* has been used to count fish schools in the eastern tropical Pacific (McClendon 1968) and in the California Current area (Smith 1970). For recent reviews of the use of echo sounders and sonars for fishery research, consult Forbes and Nakken (1972) and Cushing (1973).

The work presented here is a method for quantifying sonar records and further using these records for estimating the size of pelagic fish stocks. The paper is divided into four sections:

1. The section entitled "Sources of sampling variability" describes the scale and variance of measured acoustic parameters of fish schools, i.e., horizontal fish school dimensions and peak target strength or echo intensity. It further discusses major biases affecting the measurement of these values.
2. The estimation of fish biomass in an aggregation involves the determination of a conversion factor by which the detected horizontal area of a fish school may be multiplied. Experiments to determine the weight of the fish under a square meter of school area are described in a section entitled "Horizontal school area to biomass conversion factors."
3. An automated data acquisition system is described in the third section.
4. The results of a paired sonar survey of the Los Angeles Bight, utilizing the automated system and a biomass factor determined during the cruise, are presented and discussed in the fourth section.

This report is the second in a series describing

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progress on a number of objectives established in early 1968. In order to develop "sonar mapping" as a stock assessment tool, it was decided that such a system should be able to: 1) count the number of schools per unit area in the upper mixed layer from a ship proceeding at 12 knots, 2) measure the horizontal size of each fish school, 3) calculate the biomass of each school, 4) estimate the size of individual fish within a school, and 5) distinguish the northern anchovy from all other schooling species.

Smith (1970) developed a technique for "mapping" fish schools in the area where the northern anchovy, *Engraulis mordax*, is abundant off the coast of southern California. Sonar mapping differs from echo sounding; with sonar, estimates can be made of the number of fish schools per unit area, of their horizontal dimensions, and of the degree of aggregation of fish schools. We do not routinely estimate depth of the school in the water column, nor thickness of the school in the vertical plane. Hull-mounted echo sounders provide estimates of the number of schools per line transect deeper than 4 m, measures of chords across the horizontal dimension of the school in the plane of ship travel, depth in the water column, and thickness or vertical height of the fish school. Experience indicates that the process of "sonar mapping" encounters one or two orders of magnitude more fish-school targets per unit of ship time as compared to echo sounding from the same vessel. It is important to emphasize that this technique was developed because fish schools are frequently found in the upper mixed layer of the ocean where echo sounders are relatively ineffectual at counting or measuring them.

In the first report on this project, Smith (1970) described a series of experiments designed to determine the feasibility of the use of sonar to count and measure the size of pelagic fish aggregations (objectives 1 and 2). Optimum instrument settings were determined for source level, receiver gain, pulse length, transducer bearing, transducer directivity, and range. Methods were developed for correcting target width (dimension measured on axis parallel to ship's track) for the effect of the beam angle and for correcting target count "edge biases." Since no target was counted unless it lay entirely within a specified range, the latter adjustment was made to compensate for the narrowing possible interval of detection for larger targets.

Holliday (1972, 1974) investigated the frequency domain processing of fish school echoes using experimental equipment brought aboard the *David Starr Jordan*. By detecting and measuring Doppler spread, Holliday was able to calculate tail beat amplitudes of schooled fish and, indirectly, their length (objective 4).

Holliday also examined the resonance structure of pulse returns from fish schools and was able to detect the presence or absence of a swim bladder in the school constituents. This information, when supplemented by observations on school behavior and free vehicle camera drops, may be used to distinguish anchovy from other pelagic schooling organisms in a sample taken randomly from targets encountered during a survey (objective 5). The statistical base thus obtained would be applied to the entire survey.

The California Department of Fish and Game (CF&G) has been engaged in sea surveys using sonar methods since 1967 (Mais 1974). Its approach has been the collection of large amounts of data and its interpretation, while the work at the Southwest Fisheries Center (SWFC) has been in the isolation of sampling errors and the development of an automated hydroacoustic data acquisition and processing system. As such, the two groups complement each other with field experience and technological development.

SOURCES OF SAMPLING VARIABILITY

We have made the assumption that quantitative errors associated with system instrumentation are small in comparison to errors generated by sampling an adult schooling population whose behavior is little understood. For this reason, we monitored our sonar system response when it was operated in a variety of circumstances and changed that system in answer to practical rather than theoretical considerations. Using operating techniques developed in 1968, school size frequency distributions were generated and a lower detectable size threshold defined; school target strengths were calculated and compared with similar work conducted by the Navy and the CF&G; the relationship between the detected occurrence of pelagic fish schools and bottom topography was investigated; and the variable range of detection of schools due to internal waves was studied (Smith[3]).

[3]Smith, P. E. 1973. The effects of internal waves on fish school

Based on Smith's (1970) work, sonar mapping cruises aboard the *David Starr Jordan* were conducted with a 30-kHz sonar unit directed 90° to starboard and 3° down. The sampled range band was 200 to 450 m from the transducer. The receivers were rebuilt using solid state circuitry with the remaining system as described by Smith (SIMRAD 580-10 Scientific Sonar and Sounder).[4]

Target Size

Frequency distributions of fish school sizes were generated from data taken on several cruises (April-May, November, December 1973; and March-April 1974) using the maximum difference between the leading and trailing edge of the echo envelope, corrected for pulse length, on an axis perpendicular to the ship's track. The calculation of target widths (measured on an axis parallel to the ship's track) was discontinued due to uncertainties in choosing the effective beam width (see Smith 1970), fluctuations in the ship's speed, and the inability to quantify other factors which may affect apparent target width (i.e., target strength).

School size distributions (based on range differences) remained nearly constant during several sampling periods and agreed well with a much larger sample collected by the CF&G. A total of 4,355 sonar targets were counted and assigned to size classes on three cruises approximately 6 mo apart. Ten-meter class intervals were used and frequencies were corrected for recording edge bias employing the method described by Smith (1970). This bias is encountered when one excludes targets which do not entirely occur within the observation band. Thus, frequencies of targets other than point sources, are underestimated by virtue of the fact that their physical size limits the probability of their detection. To determine unbiased relative proportions of target sizes, one must correct observed target count (those targets which lie entirely within the observation band) to a count of targets whose centers lie within the observation band.[5]

In developing a correction for recording edge bias, a diagram may be useful. In Figure 1 a school of diameter d is shown at the maximum and minimum ranges of detection for an observer on a ship sampling an observation band of k units. The difference between the maximum and minimum range of detection is $k - d$ units.

Let A represent the event that a school of d diameter has its center within an observation band of k units. Let B represent the event that a school of d diameter is not intersected by either edge of the observation band. Then the probability of event B occurring given that event A has occurred may be expressed:

$$P[B/A] = \frac{k - d}{k}.$$

Further, let N_d represent the count of targets of diameter d who lie entirely within the observation band. Let N'_d represent the count of targets of diameter d whose centers lie within the observation band. Since N'_d represents both edge intersected and non-edge intersected targets of diameter d, the portion of non-edge intersected targets may be estimated by:

$$N_d = N'_d P[B/A] = N'_d\left(\frac{k - d}{k}\right).$$

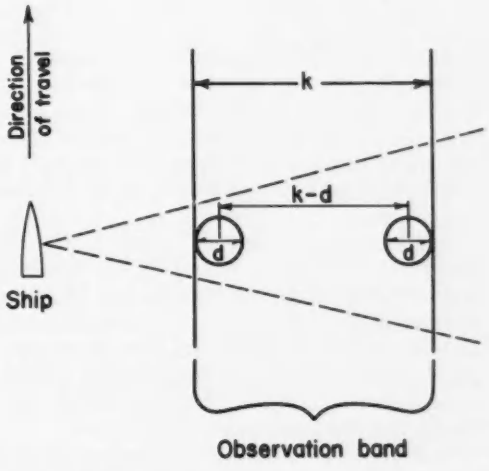

FIGURE 1.—Plan view of sonar mapping technique showing maximum and minimum ranges of detection for a target of diameter d within an observation band of k units.

mapping. Presented at the ICES-ICNAF-FAO Symposium on the Acoustic Methods in Fisheries Research, Bergen, Norway, Contrib. No. 8, 13 p.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]It is assumed that range-dependent, size-specific target losses are a minimum for the observation band sampled (Smith 1970). A similar study expanded to include the effects of target strength on detection ranges would be of value.

In actual practice N_d is tabulated. N'_d is then estimated by rearranging the above expression:

$$N'_d = N_d\left(\frac{k}{k-d}\right)$$

where N_d = observed class frequency
N'_d = edge corrected class frequency
k = extent of the observation window in meters (usually 250 m)
d = mean class diameter in meters.

As an example, when using a 250-m observation band, a 50-m target may be entirely detected over 200 m of that band, whereas a 100-m target must occur within a band of only 150 m to be detected. If one counts 10 50-m targets and 3 100-m targets, the counts, when corrected for edge bias, will be $10(250)/(250-50) = 12.5$ and $3(250)/(250-100) = 5$, respectively.

Horizontal school area is calculated by multiplying N' by the area of a circle whose diameter is equal to the class mark. The calculation is based on the assumption that with an increasing sample size the school dimension perpendicular to the ship's track will approximate the diameter of a circle whose area is equal to the area of a given school, however irregularly shaped. This assumption contains the condition that the orientation of a sample of schools is random and in no way related to that of the survey ship.

The resulting cumulative frequency diagram (Figure 2) would indicate that over 50% of the schools are less than 30 m in diameter while 90% of the horizontal school area is contributed by schools larger than 30 m in diameter. Mais' (1974) experience with over 23,000 schools (corrected for edge bias) in the same survey area indicated a similar distribution with a mode at 30 to 40 m (Figures 2, 3).

Smaller schools (<20 m in diameter) were likely to be undersampled by both the National Marine Fisheries Service (NMFS) and CF&G as the probability of their detection decreases faster with range than larger schools. Even if an exponential model of target size obtains in nature, schools smaller than 20 m would contribute little in amounts of horizontal school area.

The significance of a negative bias in the lower end of the observed school size distribution may be evaluated by fitting a power curve to that portion of the distribution between 15 and 165 m.

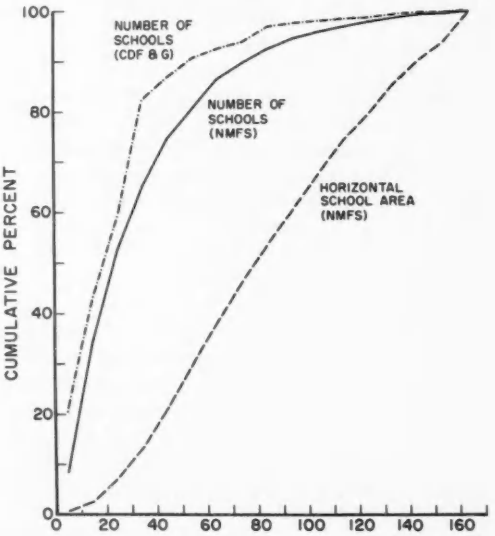

FIGURE 2.—Cumulative frequencies of sonar-detected fish schools by size and their contributing horizontal area (NMFS data only). The two modes in the CF&G data curve, drawn from a much larger sample (5×), might suggest either a systematic sampling error or optimum fish school sizes.

The equation, derived by a least squares fit, assumes the following form:

$$y = ax^b.$$

Using the NMFS sample of 4,355 targets:

$$N'_i = 428{,}864\ (D_m)_i^{-1.874}$$

where N'_i = edge-bias corrected target frequency within class i
$(D_m)_i$ = mean diameter of class i in meters.

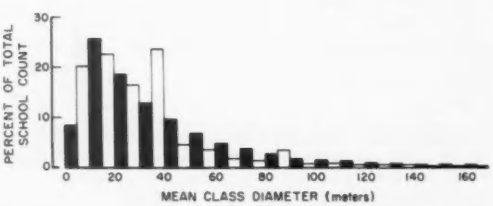

FIGURE 3.—Percent of total school count by size class. NMFS data are represented by the shaded bars; the open bars are calculated from CF&G data.

The correlation coefficient (r) = −0.969. Table 1 summarizes horizontal school area contributions by size class for observed frequencies corrected for edge bias and for frequencies derived from the exponential model. In both cases more than 90% of the area was contributed by schools larger than 20 m. The importance of horizontal school area is that it is probably proportional to the tonnage of fish in schools and, in this sense, decreases the significance of any bias in the counts of small schools.

TABLE 1.—Cumulative percent of total horizontal school area contributed by size class for observed frequencies (corrected for edge bias) and for frequencies derived from an exponential model.

Mean class diameter	N	N'	Model	Cumulative % A	
				Observed	Model
5	420	429	21018	0.09	4.24
15	1,247	1,347	2682	2.48	9.12
25	843	937	1030	7.17	14.32
35	556	647	548	13.52	19.73
45	403	491	342	21.50	25.32
55	277	355	235	30.11	31.05
65	182	246	172	38.44	36.91
75	124	177	131	46.33	42.88
85	86	130	104	53.98	48.98
95	57	92	84	60.63	55.09
105	47	81	70	67.79	61.39
115	32	59	59	74.07	67.72
125	22	44	50	79.58	74.03
135	19	41	44	85.61	80.42
145	11	26	38	90.02	86.89
155	7	18	34	93.57	93.53
165	10	29	30	99.99	99.99
>165	12				
	4,355				

Diurnal and Seasonal Effects

Time specific frequency distributions were drawn for data collected on cruises in April-May and in November 1973 for the purpose of discerning variations in sizes and detection of schools during various times of the day. While variations were noticed, their pattern was neither pronounced nor consistent from cruise to cruise. This is not to say that daily changes in schooling behavior do not exist, but that our data base is insufficient, at present, to delineate them. In the evening, discrete, well-formed schools of anchovy have been observed to disperse into a thin scattered layer but no program of study on this problem has been undertaken.

The data base is insufficient to detail seasonal changes in school size distributions, although, from communication with Mais and several commercial fishermen, we have reason to expect somewhat larger schools in the fall and smaller, scattered schools in the spring. Mid-spring is considered to be the main spawning season of the northern anchovy.

Target Strength

Acoustic target strength is proportional to the ability of an object or group of objects to reflect sound waves. Acoustic reflections from schools of fish are not presently well enough understood for rigorous characterization of the biomass of a fish school by the use of sonar. Nevertheless, we have measured apparent fish school target strengths with the objective of providing data which may lead to the quantification of fish schools in terms of total biomass.

Peak echo amplitudes were collected and corrected for propagation and absorption losses by employing the active sonar equation:

$$EL = SL - 2TL + TS$$

where EL = echo level in decibels (dB)
SL = source level in decibels, reference 1 μbar at 1 m
TL = transmission loss in decibels
TS = target strength in decibels.

Solving for target strength and using signal voltage level as a measure of echo level:

$$TS = 20 \log V - k + 40 \log R + 2 \propto R$$

where V = peak echo signal amplitude in volts
k = calibration coefficient which is the algebraic sum of source level, receiver sensitivity, and system gain expressed in decibels
$40 \log R + 2 \propto R$ = range dependent transmission loss (assuming spherical losses as in a homogeneous fluid) where R = midrange of target (as an approximation of the (location of peak echo amplitude), and $\propto$ = absorption coefficient expressed in decibels per meter.

Figure 4 illustrates five samples of peak target strengths computed from data taken by the

NMFS, U.S. Navy, and CF&G. Two of the distributions are "absolute" target strength in decibels and three are relative measurements, i.e., the calibration coefficient was not included in the calculations. The range of peak target strengths observed in any one sample varies from 28 to 34 dB. The two distributions of absolute target strength were obtained with the same sonar unit aboard the *David Starr Jordan*. The value of the calibration coefficient was recomputed after hydrophone calibration between cruises and remained constant. As such, the favorable comparison between the samples may be deceptive. The CF&G data were obtained and processed in a similar fashion using a 38-kHz sounder.

The theoretical target strength of a fish school has been discussed by Weston (1967) and Uretsky (1963). Modeling a fish school as a two dimensional array of bubbles in a liquid, both Weston and Uretsky predicted a sharp drop in response

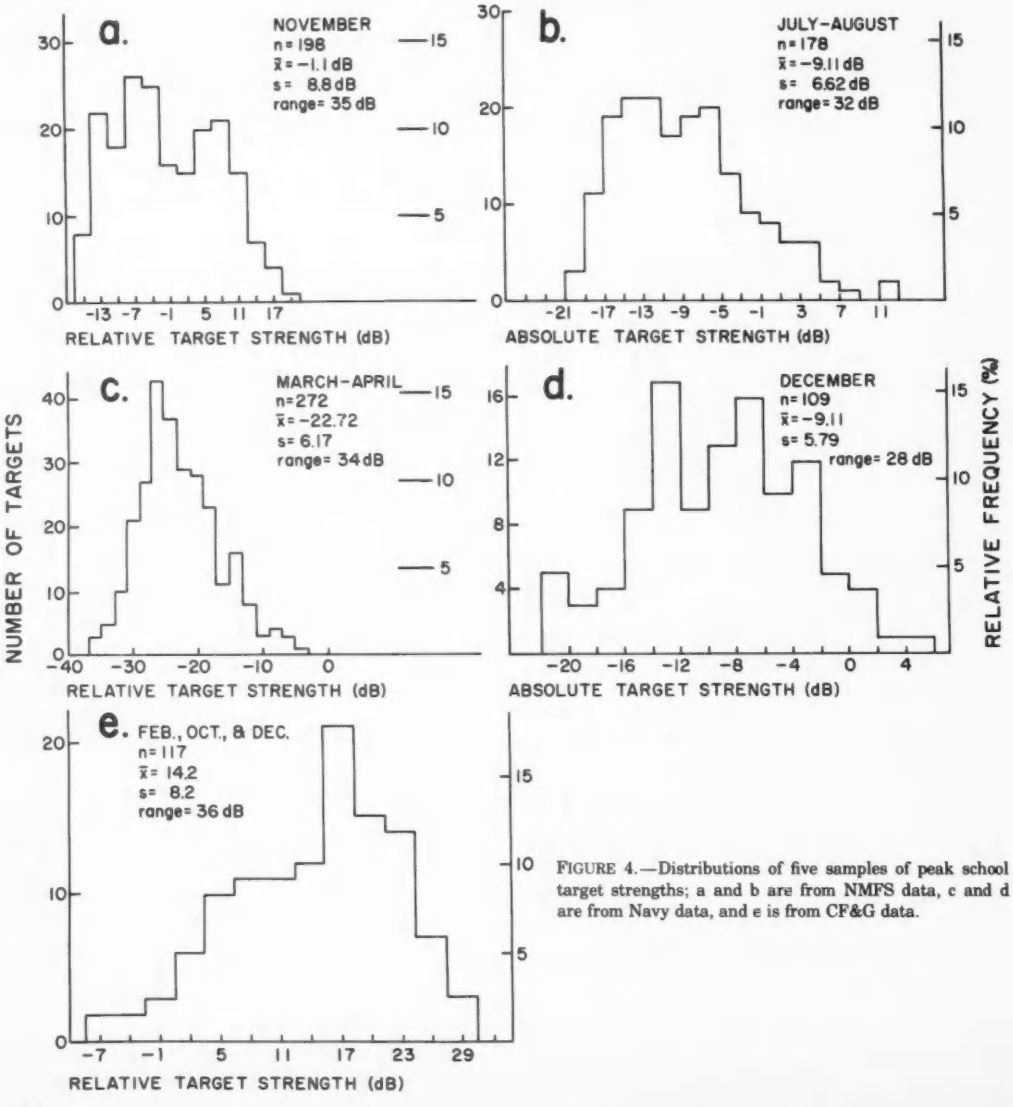

FIGURE 4.—Distributions of five samples of peak school target strengths; a and b are from NMFS data, c and d are from Navy data, and e is from CF&G data.

with increasing frequency above resonance. Using this approach, the energy scattered by the boundary of a fish school ensonified (irradiated acoustically) with 30 kHz sound becomes negligible.

Weston (1967) further suggested that an incoherent addition of reflected energy from individual fish may be expected as sound is transmitted across the boundary of a fish school. At 30 kHz, this component of target response becomes dominant and is reduced (or enhanced) by multiple scattering and absorption within the school.

The target response due to sound scattering by individual fish, assuming a mean wave phase interference of zero, may be calculated by summing the scattering cross sections of the fish comprising the target. Expressed in target strength, TS:

$$TS = TS_i + 10 \log n \text{ (decibels)}$$

where TS_i = the average target strength of the individual scatterer
n = the number of scatterers contributing to the total echo.

The number of scatterers contributing to the measured echo, n, may be estimated by applying observed and theoretical school densities (fish per cubic meter) to the ensonified volume. The ensonified volume may be estimated from:

$$V = \frac{c\tau}{2}(d)(D) \text{ (cubic meters)} \qquad (1)$$

where $\frac{c\tau}{2}$ = the range extent of the volume sampled by a sound pulse τ seconds long and moving at a speed of c meters per second
D = the vertical dimension of the school in meters
d = the horizontal dimension of the school.

School dimensions, D and d, are further limited by beam geometry, i.e., a school may not be fully ensonified if its dimensions exceed the effective beam width at the range of detection. The effective horizontal beam width may be estimated as that between the half-power points or:

$$2R\tan\beta$$

where R = range of detection
$\beta = 5°$ for the 30-kHz transducer used in this study.

Thus, d is the smaller of the measured horizontal dimensions or $0.175R$. Vertical dimensions of fish schools are not readily measured with sonar. However, in studying echograms of thousands of schools, Mais (1974) noted less variation in the vertical school dimension than the horizontal dimension and reported a mean school thickness of 12 m. The vertical effective beam width is estimated to be 12° or 42 m at 200-m range. If D is then assumed to be 12 m for all schools, there is no limitation imposed by the vertical beam width except that caused by vertical positioning of the school.

Using a 10 ms pulse length and estimating the speed of sound in a seawater medium at 1,500 m/s, Equation (1) becomes:

$$V = 90\,d$$

where d is the smaller of the measured horizontal dimensions or $0.175\,R$.

Mais (1974) reported visual observations of anchovy schools and estimated average packing density at 50 to 75 fish/m^3. Graves[6] analyzed in situ photographs of three anchovy schools and reported a mean density of 115 fish/m^3 at a mean spacing of 1.2 body lengths. Hewitt[7] used an idealized model of anchovy school compaction and calculated school densities of 0.5, 1.4, 6.6, 217, and 4,219 fish/m^3 at interfish distances of 10, 7, 4, 1, and 0.2 body lengths, respectively.

The target strength of an individual scatterer, TS_i may be estimated from considerations of acoustic theory and extensions of empirical measurements. Weston (1967) had shown the acoustic response of an ideal gas bubble to be essentially independent of frequency above resonance and proportional to the surface area of the bubble. When predicting the response of a fish swim bladder, Weston suggested an enhancement of

[6]Graves, J. 1974. A method for measuring the spacing and density of pelagic fish schools at sea. SWFC Administrative Report No. LJ-74-44. Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

[7]Hewitt, R. 1975. Sonar mapping in the California Current area: A review of recent developments. Unpubl. manuscr. Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038. The compaction model cited here used an anchovy of 12 cm standard length and computed the space required for the fish and a surrounding volume expressed in body lengths. The inverse of the resulting volume yields compaction in fish per cubic meter for a school of fish uniformly distributed in space.

75% due to shape distortion. Expressed in target strength:

$$TS_i = 20 \log L - 25 \text{ (decibels)} \qquad (2)$$

where L is the fish length in meters. Swim bladder volume is assumed to be 4.1% of total fish volume and the radius of a sphere of equal volume equal to 0.043 L (after Haslett 1965).

Using a standard length of 12 cm as typical of anchovy school constituents detected by sonar (Mais 1974), Equation (2) yields a TS_i of −43.4 dB. It should be noted that Equation (2) makes no provision for reflection, interference, or attenuation of sound waves by fish tissue.[8]

McCartney and Stubbs (1970) measured maximum dorsal aspect target strengths of six fish species at varying frequencies and lengths. They fit Equation (3) to their data and further showed that the swim bladder can account for practically all of the scattering over a wide band of frequencies:

$$TS_i = 24.5 \log L - 4.5 \log \lambda - 26.4 \qquad (3)$$

where λ = the wavelength of incident sound defined as $c(f)^{-1}$, where c is the speed of sound in a saltwater medium $\approx$ 1,500 m/s^{-1} and f is the frequency. For a 12 cm anchovy ensonified with 30 kHz sound, Equation (3) gives a TS_i of −43.1 dB.

Love (1971) reviewed maximum dorsal and side aspect target strength measurements made by several investigators. The data were obtained using fish from eight different generic orders, varying 100-fold in length, some with swim bladders and some without, and ensonified over a frequency range of 8 to 1,480 kHz. For dorsal aspect, Love related maximum target strength, fish length, and frequency by:

$$TS_i = 19.4 \log L + 0.6 \log \lambda - 24.9. \qquad (4)$$

For the anchovy described above, Equation (4) predicts a TS_i of −43.5 dB at dorsal aspect.

Love described the side aspect data with the following equation:

$$TS_i = 22.8 \log L - 2.8 \log \lambda - 22.9 \qquad (5)$$

or −40.2 dB for the anchovy described at side aspect.

A similar regression on target strength measurements taken from dead fish in dorsal aspect by six investigators and collated by Haslett (1965) would describe a TS_i of −49.8 dB for a 12-cm fish ensonified at 30 kHz (McCartney and Stubbs 1970). An application of the equations that Shibata (1970) used to describe his results yielded values of −42.8 dB for maximum dorsal aspect target strength and −40.0 dB for maximum side aspect target strength.

Several authors have noted that acoustic equipment commonly used by the biologist operates at frequencies (10 to 200 kHz) which generate sound at wavelengths comparable with the size of fish under study. Interferences will occur among the scattering components of a fish (swim bladder, flesh, skeleton, and organs) and may be expected to be a function of species and aspect. Further, our measurements are of peak school target strength taken from several transmissions along one tangential to the school and may not be the maximum value which would be obtained from interrogation at several angles.

Let us return now to the original calculations, i.e., the incoherent summation of echoes from an aggregation of fish which may now be expressed as:

$$TS = TS_i + 10 \log \left[q\,(90\,d)\right] \qquad (6)$$

where TS_i may vary from −50 to −40 dB, q is the school density in fish per cubic meter and may vary from 0.5 to 4,219, and d may vary from 5 m (mean diameter of the minimum class size) to 79 m (0.175 R at R = 450 m, the maximum range within the observation band). The expected range of peak school target strengths (assuming incoherent addition and no interference or absorption within the school) are listed below for four assumptions of fish target strength, TS_i:

TS_i	*Minimum* TS where q = 0.5 fish/m^3 and d = 5m	*Maximum* TS where q = 4,219 fish/m^3 and d = 79 m
−40 dB	−16 dB	+35 dB
−43 dB	−19 dB	+32 dB
−45 dB	−21 dB	+30 dB
−50 dB	−26 dB	+25 dB

where τ = 10 ms, β = 5°, and D = 12 m.

Based on a framework of several assumptions, we may expect a range of peak school target strengths of about 50 dB whose position on the decibel scale is determined from the value one assumes to be the average target strength of the individual scatterers comprising the school.

[8]Holliday (1972) reported an average swim bladder volume of 2.8% of the total fish volume for a sample of 239 anchovy. The use of this value predicts an anchovy swim bladder response of −44.3 dB.

From the data presented so far (Figures 3, 4) we may assume the most probable target strength for all schools to be −9 dB. Further, assuming that the "typical" school has a vertical dimension of 12 m and that the measured target strength is the summation of scattering strength of the individual fish ensonified with no effects from multiple scattering or attenuation, we may use Equation (6) to estimate q:

TS_i	q	*Spacing*
−40 dB	0.93 fish/m³	8.1 body lengths
−43 dB	1.86	6.5
−45 dB	2.95	5.5
−50 dB	9.33	3.4

Bottom Topography

Fixed transect surveys require that the distribution of schools be independent of fixed geographic locales whose scale is smaller than transect spacing.

A cruise in March-April 1974, was designed to test a postulated relationship between the occurrence of pelagic fish schools and bottom topography. The area chosen was the Los Angeles Bight and for the purposes of the experiment was defined as that body of water bounded by the southern California coast from Pt. Arguello to the U.S.-Mexican border and seaward by a line extending south from Pt. Arguello to a point west of San Miguel Island, thence southeast along an extension of the Santa Rosa-Cortez Ridge to a point north of the east end of Cortez Bank, thence east to the intersection of the shoreline and the U.S.-Mexican border. The survey area, excluding island masses, contains approximately 11.5×10^3 square nautical miles of sea surface area.

The "Bight" was further divided into four classes of bottom topography and transects designed to distribute survey effort within these zones as described below. The method used was to delineate and compute the combined areas of the first three categories and then assign the remaining area to the fourth general zone.

Bottom topography	*Total area (nautical miles²)*	*% of survey area*	*% of sampling effort*
Banks and seamounts	547	4.8	14.4
Basins and troughs	2,946	25.9	27.4
Escarpments and canyons	467	4.1	24.1
Slopes	7,510	65.2	34.1

Combined seas and swells in excess of 7 feet prohibited sonar operations on 1 day out of 12 and somewhat altered the distribution of survey effort. A detailed breakdown of zones and actual survey effort is listed in Appendix Table 1.

Daylight sonar tracking was accomplished during two time periods separated by 2 wk: 25-29 March, 1 April, and 15-19 April 1974. No difference in schooling behavior was detected between the two periods and results are presented for the total cruise time in Appendix Table 2. If an area was surveyed and no targets were detected, a "0" under "No. targets obs." so indicates; if an area was not surveyed during one or both time periods then no numbers are recorded in the appropriate columns. "Linear nautical miles surveyed" is the distance traversed while sonar tracking over the designated area. The observation window (250 m wide beginning at 200 m from the ship, and 90° to starboard from the ship's track) is multiplied by the linear distance traversed and divided into the number of targets observed to obtain target density, expressed in units of targets per square nautical mile.

The geographic names of various topographic features are commonly accepted and can be located on National Ocean Survey bathymetric maps (numbers 1205N-15, 1206N-16, 1306N-19, and 1306N-20) with the exception of the following features informally named for the sake of convenience: Coronado Bank (lying immediately to the east of Coronado Escarpment), San Diego Escarpment (along the west side of the San Diego trough), Cortez Escarpment (east-northeast of Cortez Bank), San Clemente Bank (a relatively deep bank northeast of San Clemente Island), Santa Rosa North and South Bank, San Nicolas Escarpment (southeast of San Nicholas Island), Santa Cruz Bank (south-southeast of Santa Rosa Island), Santa Barbara Escarpment (west of Santa Barbara Island at the southeast end of Santa Cruz Basin), Santa Barbara Bank (north of Santa Barbara Island), and Santa Monica Escarpment (along the southwest side of Santa Monica Basin).

The data fail to support the notion that the occurrence of pelagic fish schools can be related to bottom topography over which they are detected. Mean target densities (number of targets observed per square nautical mile) were calculated for the four classes of bottom topography and although these densities range from 2.98 (banks and seamounts) to 8.23 (escarpments and can-

TABLE 2.—A comparison of the variance in detected target densities within the classes of bottom topography (zone) and between the zones. Probability <0.5 that there is an other than random relationship between the four classes of bottom topography and detected school occurrence rates (target densities).

	Targets observed (no.)			Target density (targets/nmi²)		
Zone	25 Mar.-1 Apr.	15-19 Apr.	Total	25 Mar.-1 Apr.	15-19 Apr.	Total
Banks and seamounts	36	2	38	3.57	0.75	2.98
Basins and troughs	117	244	361	4.42	12.08	7.74
Escarpments and canyons	29	229	258	2.11	12.81	8.23
Slopes	194	69	263	8.55	3.25	5.98

	Sum of squares	Degrees of freedom	Means of squares	*F*
Within zone	72.9765	29	2.5164	
Between zones	2.9932	3	0.9977	0.40

yons), an analysis of the variance would suggest that there is no variance between the zones that could not be explained by the existing variability within the zones (Table 2).

HORIZONTAL SCHOOL AREA TO BIOMASS CONVERSION FACTORS

Fish Trap Experiment

The first effort toward determining a horizontal school area to biomass conversion factor was conducted in 1970 and briefly described in the discussion following the presentation of Smith's (1970) paper and transcribed in the publication of that paper.

An acoustically transparent trap (Figure 5) was constructed and live northern anchovy enclosed. Two groups of fish were ensonified and their horizontal area measured. A 354-kg group yielded a target strength within the range frequently encountered while a 2,017-kg group's target strength was well above that observed in nature for schooling fish.

Ensonification of additional weight groups was not possible due to the presence of predators and attempts at visual observation of the fish aggregation using a manned submersible eventually destroyed the trap. A value of 31 kg of fish biomass/m² was derived from the 354-kg group and judged to be our best estimate (Table 3). Mais (pers. commun.) reports from his experience

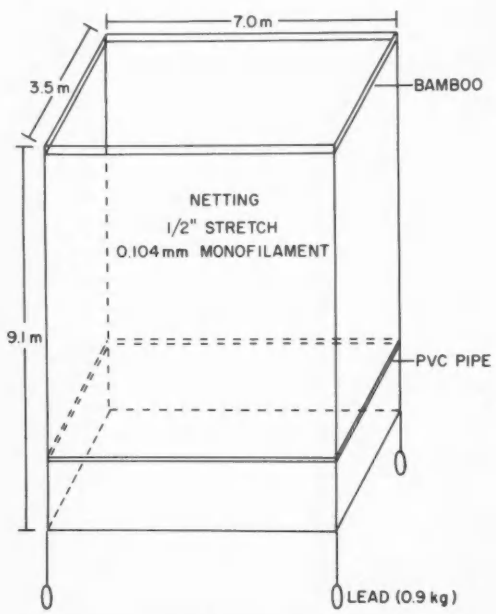

FIGURE 5.—Diagram of an acoustically transparent trap for ensonifying a group of fish of known size and weight.

TABLE 3.—Computation of a horizontal school area to biomass conversion factor from data gathered during the fish trap experiment (February 1970).

	50-fish sample		354-kg group		2,017-kg group	
Weight class (g)	No. of fish	% of sample weight	No. of fish	Total weight (g)	No. of fish	Total weight (g)
10	24	33.8	11,925	119,652	68,175	681,746
15	15	31.7	7,481	112,218	42,626	639,389
20	9	25.4	4,496	89,916	25,616	512,318
25	1	3.5	496	12,390	2,824	70,595
30	0	0	0	0	0	0
35	0	0	0	0	0	0
40	1	5.6	496	19,824	2,824	112,952
Total	50	100.0	24,894	354,000	142,065	2,017,000

		354-kg group		2,017-kg group	
Surface area[1]		[2]Mt/m²	No./m²	Mt/m²	No./m²
11.39		0.031	2,190	0.177	12,473

[1]The fish are schooled in an ellipse with a major radius of 2.90 m and a minor radius of 1.25 m (surface area 11.39 m²).
[2]Metric tons per square meter.

a representative anchovy school compaction around 50 fish/m³ or a distance of two body lengths between fish. Using a single fish weight of 18 g and an average school thickness of 12 m (Mais 1974), one obtains a horizontal school area to biomass conversion factor of 8.4 kg/m².

Charter Boat Experiment

A second experiment was designed and executed in late summer 1974, to relate measured school size, calculated target strength, and school compaction. Purse seine boats were chartered to make directed sets on fish schools first ensonified by the acoustic system aboard the *David Starr Jordan*.[9] Target strength and school size were calculated from the observation. The fishing boat supplied information on the tonnage caught and the portion of the school taken. Using these data, a biomass conversion factor was calculated for each school by dividing the total estimated school tonnage by a circular area based on the difference between its near and far ranges.

Fifty-two sets were judged to be the minimum sample size necessary to distinguish between two estimates of the portion of detectable pelagic aggregations that are schools of northern anchovy. Squire (1972), using data from 6 yr of observations from several commercial air spotters, reported that at least 50% of the surface schools off southern California can be expected to be anchovy. Mais (pers. commun.) estimates that 90% of the schools sampled by mid-water trawl are anchovy.

Seventy-six sets were made landing 1,901 short tons of anchovy; 63 were directed by the *David Starr Jordan* and 13 directed by the State of California's RV *Alaska*. Forty-nine positive data points were tabulated from the *David Starr Jordan*'s work and eight from the *Alaska*.

Average target size was 119 m (as measured by the difference between the near and far ranges on a line perpendicular to the ship's head) with a range from 31 to 305 m. Average peak target strength was +5.18 dB (as calculated from peak amplitude and range dependent losses) with a range from −9 to +18 dB and a SD of 5.63 dB.

Practical considerations forced us to expend a larger portion of effort on schools of larger than average size and target strength. This circumstance accounts for the fourfold increase in median target size and a 15-dB increase in mean target strength over a sonar-generated data base reported earlier. In addition, this sample was chosen from a detected school population whose acoustic dimensions were, in general, larger than that experienced on previous cruises.

To facilitate the direction of sets, the observation window was increased from 250 to 500 m wide and moved 100 m closer to the vessel. A time-varied gain increase was also accomplished in the receiver previous to signal display on an oscilloscope. Either or both of these changes to the sonar system configuration could produce circumstances under which similar data distributions would appear to be different. Point scatters encountered when plotting target size versus target strength, target strength versus horizontal school area to biomass conversion factor, and target size versus horizontal school area to biomass conversion factor are too wide to detect a relationship between these school parameters.

A distribution of horizontal school area to biomass conversion factors is presented in Figure 6. The distribution is skewed right with an arithmetic mean of 15.16 kg/m². While no relationship is as yet demonstrated between individual target strengths and horizontal school area to biomass conversion factors, the data have contributed to a refinement of a general conver-

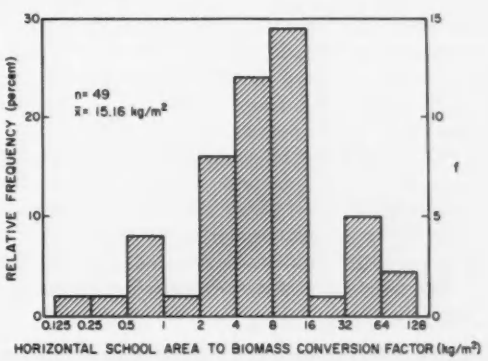

FIGURE 6.—Distribution of horizontal school area to biomass conversion factors obtained from the charter boat experiment.

[9]Contracts were let for a total of 104 sets assuming 50% success rate for positive sets and a permit was secured from CF&G to land 2,500 tons of anchovy during the experiment. A charter agreement was written establishing criteria for the successful bidders as minimum tonnage bid with the proceeds from any excess tonnage, not to exceed the permit, to be given to the State. In addition, each boat was guaranteed a fixed fee over and above the proceeds from the landed fish.

sion factor based previously on only one data point.

Eight horizontal school area to biomass conversion factors calculated from sets directed by the *Alaska* have a range from 10.14 to 30.22 kg/m^2 with a mean value of 18.42 kg/m^2. The *Alaska* participated in the experiment during the last 2 wk when only large schools were available in shallow water.

AUTOMATED HYDROACOUSTIC DATA ACQUISITION AND PROCESSING SYSTEM

In an effort to reduce observer subjectivity in the collection of large amounts of sonar data necessary for the isolation of sampling errors and biases, a decision was made to develop the capability to automatically count and measure the horizontal dimensions of sonar targets. Peak echo amplitude was also to be measured with the intention of eventually relating it to school compaction and depth.

A digital PDP8/I computer with an additional 16k memory, an analog-to-digital converter and a teletype terminal were acquired on loan from the Naval Undersea Center at San Diego. Using this gear, a project was undertaken which would allow us to do automatically what we were doing manually but with the additional benefits of real-time target strength calculation and rapid raw data processing.

The raw data used for hand target collection is in the form of a paper record containing a field of parallel lines, each line being an incremental distance along the survey track. If the amplitude of the signal is sampled during the recording of one of these lines, at a sample rate of 750 samples/s (velocity of sound/two-way path length), the result is a record of the instantaneous echo amplitude at 1-m increments along a line perpendicular to the survey track.

When several of these lines have been recorded, the result is a data field which is a numerical counterpart of the paper record. Once the word "target" is defined numerically, the number of targets in this field can be counted.

The numerical definitions used for this purpose are:

Threshold (THS) = some signal amplitude greater than the average reverberation or noise level.

Target line = at least five consecutive samples greater than THS, preceded and followed by five samples below THS.

Target block = two target lines which have at least five coincident and consecutive samples greater than THS.

Target = a target block + N additional coincident target lines, bounded by noise (signal less than THS).

The threshold, for the initial program was a predetermined constant. The five sample target line is selected on the assumption that a 5-m target may be the smallest significant unit. The two line target block is selected since random or asynchronous noise greater than THS can cause a target line, but will rarely cause at least five coincident samples on consecutive lines. Three consecutive lines of data are stored in the memory of the PDP8/I computer. As each new line of data is stored it is tested for the presence of target lines. When a target line is found, the amplitude of the samples is compared and the value of the peak amplitude is stored in the first data point location.

The newest data line is then compared with the previous one and any occurrence of a target block is recorded in the block register. The previous data line is compared with the oldest data line and, with the information in the target block register, the following decisions are made:

1. Is the target block the beginning of a new target? If so, assign it a number and record its initial range, final range, and peak amplitude in the temporary target storage register.
2. Is the target block the entire target? If so, store its information in the final target storage field with the current time and the ship's speed.
3. Is the target block part of a previous target? If so, update the temporary storage information.
4. Is the target block the end of a previous target? If so, update the temporary information and store in final storage.

Additional logic decisions are required if two or more previously recorded individual targets later merge to form a single target, or if the inverse should occur.

There are four analog data input lines to the

system which are multiplexed and sampled at appropriate times by the analog-to-digital converter. These are:

The start pulse—the trigger pulse for the sonar transmitter.
The sonar signal—the 1,000 cycle band width detected video from the sonar receiver.
The ship's speed—a DC voltage from the ship's log proportional to speed.
The hour mark—a pulse from the ship's precision simplex clock system occurring at the end of each hour.

The start pulse initiates the program, which then counts 200 sample times before recording data. Two hundred fifty samples are then taken between 200 and 450 m, to be operated on by the program as previously described. A running count of the number of start pulses occurring after the beginning of each new hour is kept and used as a time base for all events recorded during that hour. During data reduction, this count is divided into 60 min and used to provide absolute time data.

The ship's speed is recorded with each target, and may be used to calculate the area surveyed. It is used in the data collection program to determine when a hydrographic and/or biological station has been reached and to suspend data recording while on station; start pulses continue to be counted, however, thus the time at the beginning and end of the station is recorded.

In shipboard operation, the system requires no attendance. Prior to leaving the dock, the computer is started, and the hour counter is preset to the current time. The sonar system is then started and may be left in operation 24 h a day or turned off at night. In either case, the data collection program will begin sampling automatically at 0800 each morning and continue until 1600 each afternoon, except while on station. There are six memory storage fields in the PDP8/I of 4,096 words each. One field is used for programming and temporary data storage. The other five fields provide final storage for 3,300 targets, at six data words per target. At the end of the day (1600 h) the data collection program in field zero is replaced by a general computational program used in the PDP8/I called FOCAL. This program change is accomplished automatically from a prerecorded magnetic tape cartridge. With FOCAL programming, the stored target data is now reduced, summarized, and dumped onto peripheral mass storage capable of holding the entire cruise.

When the output is finished, the collection program is reread into field zero, and the computer waits for 0800 h the following morning to again begin data recording.

Field testing of this system was conducted in July 1974, by comparing computer listings of events with the corresponding wet paper records. The system proved to have a greater resolution than was felt necessary and the criteria for a target block changed to two coincident and consecutive samples above threshold. Ten samples below threshold rather than five were judged adequate to terminate a target on any given line. A variable threshold based on an integrated value of volume reverberation is being developed.

The system was field tested under a wide variety of conditions and judged satisfactory for our requirements. Figure 7 describes a cumulative frequency diagram for school count and horizontal school area. A median school size of 30 m agrees with data from previous cruises.

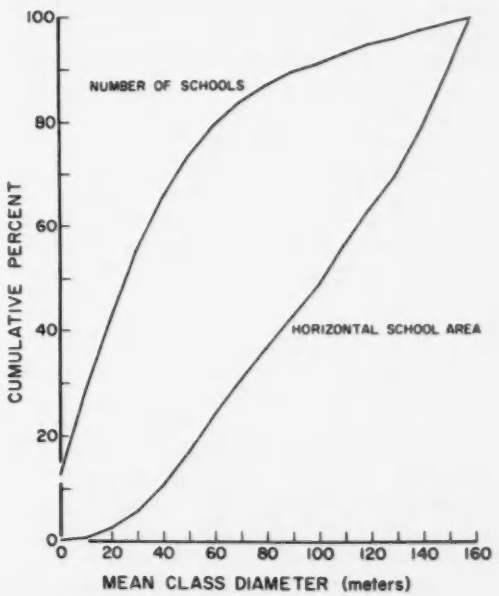

FIGURE 7.—Cumulative frequency diagram of school count and horizontal school area from a sample taken during the field test of an automated sonar system in July 1974.

AUTOMATED SONAR SURVEY

An automated sonar survey of the Los Angeles Bight was accomplished during the last 2 wk of the charter boat cruise. A 721-nautical-mile track (Figure 8) was transected two times providing a 3.4% areal sample of the 11,500-mile² Bight. Each track (1.7% sample) was processed as a separate survey.

Appendix Table 3 lists target counts on tracks 1 and 2 by target size and mid-range. Target size refers to the maximum dimension normal to the ship's track and is calculated from the difference between the leading and trailing edges of the echo envelope corrected for the pulse length (15 m at 10 ms pulse length). The first mode, common to both tracks at a target diameter of 30 m, is consistent with earlier data collected by NMFS (approximately 4,500 targets) and CF&G (approximately 23,000 targets). A second mode occurring at a school diameter of 250 m is also common to both tracks. This mode has not been seen before or during any season in any year since sonar activities were initiated off southern California. An explanation for the mode, other than the reflection of an optimum school size, is that it may be a bottom reverberation mode particular to the observation window used on the survey.

Bottom reverberation, as logged by the system, was collected for 2 h over water depths of approximately 100 m during the cruise. Distributions of target size, midrange, and target strength are shown in Appendix Table 4. Notable are two size modes at 50 and 225 m, an optimum midrange of 450 m, and an average target strength of +5 dB.

Targets contributing to the 250-m size class mode have a midrange mode of approximately 450 m for both tracks 1 and 2. Average target strength was +7 dB for the subsample. This information reinforces the theory that the 250-m size class mode is caused by false targets caused in turn by bottom reverberation. Changes in the sonar system operating parameters (i.e., the enlargement of the observation window and the addition of a time gain circuit) are assumed to be responsible for the variation in system response. These changes were made to facilitate the fish biomass work and will not be in effect during the sonar surveys to be conducted on a series of California Cooperative Oceanic Fisheries Investigations cruises beginning in November 1974. Operating procedures will be the same as used for the initial field of testing of the automated hydroacoustic data acquisition and processing system.

Since those targets which begin or end beyond the observation band are not counted, an edge bias exists which is a function of the target size and the extent of the observation window. Frequencies within target size class intervals were corrected for edge bias by the following formula:

$$N'_d = N_d \frac{500}{500 - d}$$

where N_d = frequency of observation within a given size class
N'_d = frequency corrected for edge bias
d = mean class diameter.

The largest school size corrected for edge bias was 160 m (target size distributions from previous cruises, CF&G and NMFS, indicate that 160 m includes the 99th percentile). Table 4 lists observed frequencies, edge corrected frequencies, and horizontal school area contributions for size classes up to a maximum mean class diameter of 160 m.

The total detected school area was 2.6×10^6 m² for track 1 and 1.4×10^6 m² for track 2. Integrating over the entire survey area by simple proportion, assuming no stratification, and using a conversion factor of 15.16 kg/m², biomass estimates of pelagic schooling fish in the Los Angeles Bight were calculated at 2.30×10^6 metric tons and 1.23×10^6 metric tons for tracks 1 and 2, respec-

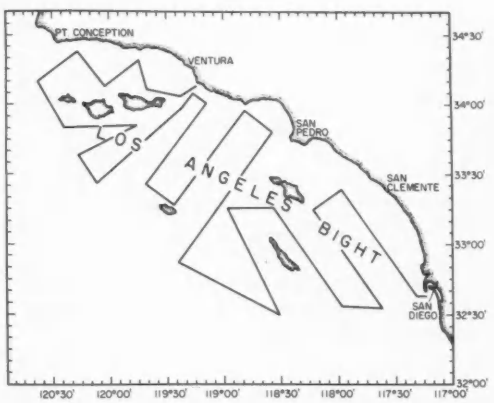

FIGURE 8.—Los Angeles Bight including a 721-mile sonar survey track transected twice, 17-26 September 1974.

TABLE 4.—Observed frequencies, edge corrected frequencies, and horizontal school area contributions for size classes (metric tons, mt) up to a maximum of 160 m school diameter.

Class limits (mt)		Mark	N (f)	N'	$\%\Sigma N'$	Cum. $\%N'$	$N'A$ $(mt)^2$	$\%\Sigma N'A$	Cum. $\%N'A$
Track 1									
−5	5	0	35	35.000	5.171	5.171	0.000	0.000	0.000
5	15	10	74	75.510	11.156	16.327	5,930.557	0.229	0.229
15	25	20	86	89.583	13.236	29.563	28,143.434	1.091	1.321
25	35	30	89	94.680	13.989	43.553	66,925.949	2.594	3.916
35	45	40	68	73.913	10.920	54.473	92,881.869	3.601	7.517
45	55	50	47	52.222	7.715	62.189	102,538.093	3.975	11.493
55	65	60	36	40.909	6.044	68.234	115,667.729	4.484	15.978
65	75	70	30	34.883	5.154	73.388	134,248.290	5.205	21.183
75	85	80	21	25.000	3.693	77.081	125,663.706	4.872	26.056
85	95	90	21	25.609	3.783	80.865	162,922.228	6.317	32.373
95	105	100	18	22.500	3.324	84.190	176,714.586	6.851	39.225
105	115	110	12	15.384	2.273	86.463	146,204.868	5.668	44.894
115	125	120	15	19.736	2.916	89.379	223,218.425	8.655	53.549
125	135	130	13	17.567	2.595	91.975	233,178.346	9.041	62.590
135	145	140	12	16.666	2.462	94.437	256,563.400	9.947	72.538
145	155	150	14	20.000	2.955	97.392	353,429.173	13.703	86.242
155	165	160	12	17.647	2.607	99.999	354,815.170	13.757	99.999
Total			603	676.815			2,579,045.851		
Track 2									
−5	5	0	33	33.000	7.902	7.902	0.000	0.000	0.000
5	15	10	46	46.938	11.240	19.143	3,686.562	0.267	0.267
15	25	20	57	59.375	14.218	33.362	18,653.206	1.353	1.621
25	35	30	50	53.191	12.738	46.100	37,598.848	2.729	4.350
35	45	40	39	42.391	10.151	56.252	53,270.484	3.866	8.217
45	55	50	39	43.333	10.377	66.629	85,084.801	6.175	14.393
55	65	60	24	27.272	6.531	73.160	77,111.819	5.597	19.990
65	75	70	24	27.906	6.683	79.843	107,398.632	7.795	27.786
75	85	80	8	9.523	2.280	82.124	47,871.888	3.474	31.261
85	95	90	8	9.756	2.336	84.461	62,065.610	4.505	35.766
95	105	100	8	10.000	2.394	86.855	78,539.816	5.700	41.467
105	115	110	8	10.256	2.456	89.312	97,469.925	7.074	48.542
115	125	120	6	7.894	1.890	91.202	89,287.370	6.481	55.023
125	135	130	5	6.756	1.618	92.820	89,683.979	6.509	61.533
135	145	140	9	12.500	2.993	95.814	192,422.550	13.967	75.500
145	155	150	4	5.714	1.368	97.182	100,979.763	7.329	82.830
155	165	160	8	11.764	2.817	99.999	236,543.446	17.169	99.999
Total			376	417.576			1,377,668.706		

tively. Identification of the fish is not yet possible on a routine basis. However, it is assumed that the majority of schooling fish in the Los Angeles Bight are northern anchovy (Smith 1972; Squire 1972; Mais 1974).

DISCUSSION

It is our impression that the ultimate value of sonar mapping is its potential to reconstruct geographic patterns of school distributions at a moderate cost of time both in data collection and data reduction. However, before this potential can be fully realized, several problems must be recognized, investigated, and placed in proper perspective.

With regard to counting and sizing targets:

1. An edge bias has been described which will be present with any sonar system designed to count and size schools. The determination of effective detection ranges establishes a finite observation band. Larger schools tend to be undersampled relative to smaller schools; in terms of school area the bias may be significant.
2. Increasing the observation band would tend to reduce the effect of edge bias. However, the effects of target size and target strength on maximum ranges of detection should be investigated before defining the observation band. Undersampling small schools may be acceptable when considering their area contribution.
3. Effective detection ranges may also be limited by inhomogeneities in the medium caused by short-period internal waves. Smith (see footnote 3) investigated this phenomenon and suggested the only practical solution is a statistical approach

whereby the number of sound velocity profiles taken in an area-time stratum would be limited to the number of samples necessary to reduce the standard error to a uniform value for all strata. A probability of detection diagram could then be constructed from the ray trace analyses and target counts corrected by range. We have not so far considered these effects in our area of operation, however, the implication of undersampling should be investigated when designing a serious stock assessment survey using sonar.

4. Diurnal and seasonal variations in school sizes can be expected. In order to properly evaluate their affect on a stock assessment scheme the period and amplitude of these variations must be measured. The collection of a data base sufficient in size to detail these changes, as well as geographic distribution patterns by season, was the primary motivation in designing an automated data collection system.
5. While it appears that influences of bottom topography on school distribution may be neglected, there is no reason to expect areal distributions to be uniform. In fact, there is evidence from aerial reconnaissance, sonar transects obtained at long ranges (2,500 m), and fishermen that fish schools may be distributed in a highly contagious fashion similar to the distributions of fish eggs and larvae. In our opinion, this is a most important consideration in arriving at an optimum survey design. Smith[10] and MacCall[11] have approached the problem by direct measurement and simulation modeling and suggest a transect spacing of 15 miles as adequate to reconstruct groups of anchovy schools off southern California.
6. Holliday (1972, 1974) demonstrated the feasibility of sizing individual fish within schools and provided information which would aid in species identification. A development of these techniques as practical additions to a sonar survey system would reduce a presently loosely quantified factor, i.e., the percent of detected schools which can be expected to be the target species of a survey.

With regard to school target strength:

1. The target strength of an individual fish is an essential element in interpreting the measured target strength of a school. At the frequencies commonly used for sonar mapping we can expect interference of energy reflected from the various scattering parts of a fish. This makes the target strength of a fish strongly aspect dependent. Unfortunately there is presently no method of acoustically determining the aspect of individuals in a school and hence their effective target strength. As such, the maximum dorsal or side aspect target strength is generally an overestimate and the use of these values in interpreting school target strengths results in an underestimate of the number of individual scatterers.
2. We may also expect multiple scattering, shadowing, and attenuation within a school. These effects may tend to reduce or enhance the target strength of a school and cannot be evaluated until we know the effective contribution of the fish taken as individual scatterers. Love (1971) stated that the quantification of a fish school using its target strength is possible because the target strength of a school depends on the average size, number, distribution, and aspect of the individuals in the school. If the effects of the distribution of fish in space and their aspect can be removed, we may assume an average size and estimate their numbers.
3. We have assumed spherical spreading losses which may only be expected in a three-dimensional homogeneous fluid. In fact, the upper mixed layer, in which we operate our sonar, is characteristically bounded by density discontinuities which reflect and refract sound waves. The actual path of transmitted and target-reflected sound waves may not be direct as implied in the use of spherical transmission losses.

[10]Smith, P. E. 1975. Precision of sonar mapping for pelagic fish assessment in the California Current area. SWFC Administrative Report No. LJ-75-60. Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

[11]MacCall, A. 1975. Anchovy population survey simulation. Contribution No. 4, CalCOFI Anchovy Workshop, July 1975. Document on hand at the Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

Continuing development of acoustic stock assessment techniques rests on the comparison of measurements and the best available theoretical models for target strength and fish school biomass. Improved instrumentation, particularly data logging and processing equipment will make the comparison more timely and useful. The existing system will be used seasonally over the entire California Current survey area (about 200,000 nautical miles^2) in 1975. It is intended that the data base thus furnished will allow a balanced approach to such biological problems as migration and patchiness of fish schools in the context of better theory and instrumentation.

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APPENDIX TABLE 1.—Topographic breakdown of Los Angeles Bight by four classes of bottom configuration (zone) and distribution of design and actual sampling effort.

Zone and name	Area (nautical mile²)	Total area (%)	Sampling effort	
			Design (%)	Actual (%)
Banks:				
Thirtymile Bank	44.8			
Fortymile Bank	39.6			
Tanner Bank	50.2			
Osborn Bank	13.4			
San Clemente Bank	37.3			
San Nicolas Bank	125.4			
Santa Rosa N. Bank	17.7			
Santa Rosa S. Bank	34.0			
Coronado Bank	19.1			
Santa Barbara Bank	72.7			
Santa Cruz Bank	79.3			
Lasuen Seamount	13.2			
Total	546.7	4.8	14.4	9.4
Basins:				
San Clemente Basin	91.7			
Catalina Basin	540.8			
San Nicolas Basin	497.3			
San Diego Trough	264.2			
San Pedro Basin	145.6			
Santa Monica Basin	490.3			
Santa Cruz Basin	213.2			
Santa Barbara Basin	733.2			
Total	2,976.3	25.9	27.4	34.4
Escarpments and canyons:				
Coronado Escarpment and Canyon	37.3			
Catalina Escarpment	99.5			
San Clemente Escarpment	97.4			
San Diego Escarpment	38.9			
San Pedro Escarpment and Redondo Canyon	33.4			
San Nicolas Escarpment	34.2			
Santa Cruz Escarpment and Canyon	75.4			
Santa Monica Escarpment	15.5			
Santa Barbara Escarpment	23.3			
Cortez Escarpment	12.4			
Total	467.3	4.1	24.1	23.7
Slopes		65.2	34.1	32.5

APPENDIX TABLE 2.—Detected targets and target densities for four classes of bottom topography (zone) in the Los Angeles Bight.

Zone and name	No. targets obs.	Linear nautical miles surveyed	Target density (targets/nmi²)
Banks and seamounts:			
Thirtymile Bank	3	12.40	1.79
Fortymile Bank	18	16.99	7.85
Tanner Bank			
Osborn Bank	1	6.19	1.20
San Clemente Bank			
San Nicolas Bank			
Santa Rosa Bank			
Santa Rosa S. Bank			0
Coronado Bank	0	8.0	0.75
Santa Barbara Bank	2	19.8	0
Santa Cruz Bank	0	21.59	0
Lasuen Seamount	14	9.59	10.81
$\overline{\ln x}$ excluding zero values			0.9835
$S_{\ln x}$			1.1758
Basins and troughs:			
San Clemente Basin	43	22.60	14.09
Catalina Basin	84	83.99	7.41
San Nicolas Basin	135	44.19	22.63
San Diego Trough	94	58.19	11.84
San Pedro Basin	4	21.40	1.38
Santa Monica Basin	1	31.59	0.14
Santa Cruz Basin	0	23.4	0
Santa Barbara Basin	0	37.4	0
$\overline{\ln x}$ excluding zero values			1.4325
$S_{\ln x}$			1.9237
Escarpments and canyons:			
Coronado Escarpment and Canyon	1	19.40	0.38
Catalina Escarpment	15	28.19	3.94
San Clemente Escarpment	3	40.39	0.55
San Diego Escarpment	172	51.53	24.73
San Pedro Escarpment and Redondo Canyon	25	19.80	9.35
San Nicolas Escarpment	38	14.99	18.78
Santa Cruz Escarpment and Canyon	4	33.18	0.89
Santa Monica Escarpment	0	11.00	0
Santa Barbara Escarpment	0	12.4	0
Cortez Escarpment	6	6.79	6.55
$\overline{\ln x}$ excluding zero values			1.2431
$S_{\ln x}$			1.6145
Slopes	0	9.40	0
	21	20.19	7.71
	0	6.00	0
	0	6.80	0
	0	5.00	0
	0	7.99	0
	5	22.80	1.62
	0	7.80	0
	4	7.20	4.16
	9	12.39	5.38
	65	30.69	15.69
	46	16.59	20.54
	23	9.00	18.93
	21	6.20	25.09
	7	15.20	3.41
	20	4.00	37.04
	0	3.60	0
	0	3.20	0
	1	55.00	0.13
	0	5.40	0
	22	11.20	14.55
	0	27.20	0
	2	17.20	0.86
	17	15.51	8.12
$\overline{\ln x}$ excluding zero values			1.7850
$S_{\ln x}$			1.5365

APPENDIX TABLE 3.—Target counts by size and midrange detected on an automated survey of the Los Angeles Bight (tracks 1 and 2) during September 1974.

Size (m)	100-150	150-200	200-250	250-300	300-350	350-400	400-450	450-500	500-550	550-600	Total
<5	3	3	6	11	17	6	3	5	7	6	67
6- 15	4	5	7	16	26	18	7	13	14	10	120
16- 25	1	8	11	23	24	16	15	11	17	17	143
26- 35	4	3	4	15	29	21	15	11	22	15	139
36- 45		2	4	9	24	14	11	13	19	11	107
46- 55		1	3	7	8	10	10	10	21	16	86
56- 65		3	2	4	11	2	9	6	16	7	60
66- 75			1	2	7	2	7	8	27		54
76- 85		1		1	1	4	6	5	11		29
86- 95			1	3	3	2	3	2	15		29
96-105					2	2	3	4	15		26
106-115				1	1	3	3	4	8		20
116-125				3	1	2	4	4	7		21
126-135						4	1	5	8		18
136-145				1	2	3		8	7		21
146-155				1		5	5	3	4		18
156-165			1		4	3	2	5	5		20
177-175			1		1		3	6			11
176-185						2	9	11			22
186-195					1	1	11	7			20
196-205				4	1	3	12	8			28
206-215					2	2	11	10			25
216-225					1	5	14	23			43
226-235					2	3	27	25			57
236-245						3	26	22			51
246-255					1	3	31	27			62
256-265						3	34	14			51
266-275						1	21				22
276-285						2	24				26
286-295						1	23				24
296-305				1	1	2	22				26
306-315						3	16				19
316-325				1	1	1	8				11
326-335						3	4				7
336-345						1	1				2
346-355						3					3
356-365						2	1				3
366-375						3					3
376-385						4					4
386-395						1					1
Total	12	26	41	103	171	169	402	270	223	82	1,499

APPENDIX TABLE 4.—Bottom reverberation by detected size, midrange, and target strength from data collected during 2 h in 100 fathoms on 7 September 1974.

Item	Mark	*f*	Relative %	Item	Mark	*f*	Relative %
Size	25 m	9	5.4	Midrange	480	15	8.9
	50	24	14.3		500	7	4.1
	75	11	6.5		520	7	4.1
	100	9	5.4		540	1	0.6
	125	8	4.8		560	1	0.6
	150	10	6.0	Target strength	−2dB	1	0.6
	175	18	10.7		−1	1	0.6
	200	26	15.5		0	4	2.4
	225	24	14.3		1	11	6.5
	250	23	13.7		2	18	10.7
	275	6	3.6		3	21	12.4
	300	0	0		4	25	14.8
Midrange	340 m	5	3.0		5	28	16.6
	360	7	4.1		6	25	14.8
	380	6	3.6		7	6	3.6
	400	9	5.3		8	9	5.3
	420	25	14.8		9	7	4.1
	440	44	26.0		10	8	4.7
	460	42	24.9		11	5	3.0

ECONOMIC AND FINANCIAL ANALYSIS OF INCREASING COSTS IN THE GULF SHRIMP FLEET[1,2]

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ABSTRACT

The 115 Gulf of Mexico shrimp vessels used in this study were grouped into classes I (larger vessels) through V (smaller vessels) based on their type of construction, length of keel, and index of effort. In 1973, class II vessels were the only vessels able to register a positive return to owner's labor and management, $560; the other four classes registered negative returns. The payback period occurred during the eighth year due to the sale of the vessels in classes II, III, and V, whereas payback did not occur for classes I and IV. A positive rate of return on investment was experienced by the vessels in classes II, III, and V in the amount of 13.21, 2.65, and 2.63%, respectively. The internal rate of return on investment was negative for vessels in classes I and IV.

Input prices increased some 20% from 1973 to 1974 whereas production remained approximately constant and ex-vessel shrimp prices were lower. Thus none of the classes of vessels would have experienced a break-even cash flow for 1974. Increasing input cost another 10% above the 1974 level, and assuming normal production, the average vessel in class II seems to be operating at a better than a break-even level in 1975 assuming ex-vessel shrimp prices remaining constant at 1973 levels. Classes I, III, IV, and V experienced less than break-even cash flows under the same conditions in 1975.

The U.S. economy has faced some strong buffeting in recent years. In spite of temporary wage and price controls and other efforts by the administration, inflation has continued to be a major problem for most sectors. The percentage increases in the wholesale price index (including all commodities) were 4.2% from 1971 to 1972, 13.1% from 1972 to 1973, and approximately 20% from 1973 to 1974 (Board of Governors of the Federal Reserve System 1974). Since inflation can occur at different rates for different products, profit and loss positions in almost every sector or industry in the economy have been affected. Of particular interest to shrimp vessel owners are changes in the price for basic inputs used in the shrimp industry: the price index for fuel, which accounted for approximately 25% of variable costs of shrimp production in 1971 (excluding crew shares) (Hayenga et al. 1974) increased 76% from December 1971 to December 1973; and the price index for lumber, metals, and machinery and equipment (inputs used in the construction of shrimp vessels) jumped 46.5, 19.2, and 7.9%, respectively, during the same period (Board of Governors of the Federal Reserve System 1973).

With regard to prices and production in the Gulf States, in 1973 ex-vessel shrimp prices increased 33% from the 1972 figures, but landings were off from the 1972 levels by 21% (United States Department of Commerce 1974).

Due in part to the economic climate, vessel owners, managers, financial institutions, and marine resource researchers have come to rely heavily upon cost and return data in analyzing investment, financing, and profitability alternatives within the Gulf shrimp industry. But a classification problem exists because of the wide range of combinations of vessel size, construction, power, and fishing capability within the Gulf shrimp fleet and the wide range of variable costs, fixed costs, investment requirements, and profitability associated with the various vessel configurations. It is the purpose of this paper to investigate, for different vessel classes, the profitability of investing in and operating a vessel in the Gulf shrimp fleet based on data collected for the 1973 calendar year, and then with the data adjusted to estimated 1974 and 1975 levels.

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METHODOLOGY

Standard techniques of cost and return, cash flow, and break-even analysis were used in this study. A budget-generating computer program was established to assimilate and report the data according to each of the desired vessel configurations, in the form of total costs and returns budgets, unit costs and returns budgets, and projected cash-flow budgets.

The vessels were classified in terms of their average costs per pound of shrimp landed. An average cost equation was estimated using regression analysis with construction, keel length (U.S. Coast Guard registry), and effort index[4] as dummy variables. Vessels included in the sample were constructed of either wood or steel. Grouping of vessels according to keel length and effort index for use as dummy variables in the regression analysis was based on a natural frequency distribution of the vessels in the sample.

It must be stressed here that this method of classification is simply a means to group the vessels for the purpose of analysis and is not necessarily a criterion for evaluation of the performance of the different classes. Performance or profit depends not only upon unit cost but also upon unit price. Even though one class of vessels may have a higher average cost curve for a given level and type of shrimp produced, it may not necessarily produce less profit. Therefore, while the product produced may be homogeneous with respect to cost of production, it may be heterogeneous with respect to price.

DATA DESCRIPTION

Data Collection and Vessel Description

The cost and return and financial data used in this study were gathered by personal interview with shrimp vessel owners and/or managers operating from ports in Florida, Mississippi, and Texas. Additional financial information was obtained from officials of various lending institutions which engage in shrimp vessel financing. All data were for the period covering the calendar year 1973.

The original sample for this study consisted of 126 vessels. However, due to incomplete data, only 115 vessels were used in the analysis. Vessels in the sample were constructed of wood and steel, with keel lengths of from 45 to 78 feet, and from 104 to 777 horsepower. The ages of the vessels ranged from 1 to 36 yr.

Costs and Returns and Cash Flow Data

Variable cost items were separated into variable costs not directly proportional to catch: ice; fuel; nets, supplies, and groceries; repair and maintenance; and variable costs directly proportional to catch: crew shares, payroll taxes, and packing charges. Actual variable cost data reported by the vessel owners were used except for crew shares, payroll taxes, and packing charges, which were determined on the basis of reported pounds landed and gross revenues. Vessel owners paid their captains and/or crew on the basis of a percentage of pounds landed. This percentage ranged from 30% in the eastern Gulf to 40% in the western Gulf. Thirty-five percent was the average share paid and is used in the analysis.

Fixed cost items were separated into: insurance, depreciation, overhead, interest, and opportunity cost (required return to equity capital). Fixed charges for insurance and overhead are reported data. Charges relating directly to investment—depreciation, interest, required return on equity capital for costs and returns, and principal and interest for cash flow budgets—were standardized in terms of 1973 dollars in order to make valid comparisons. Since most of the vessels included in the sample were purchased new, vessel owners (some of which were shipbuilders) were asked to estimate the replacement value of their

[4]The effort index is defined as the amount of fishing power that a vessel can exert in a day fished relative to that of a standard vessel. The value for the effort index for each vessel was calculated using the formula:

$$EI_i = \frac{(HP)_i^{0.1385} \quad (LFR)_i^{0.4064}}{(38)^{0.1385} \quad (14.6)^{0.4064}}$$

where EI_i = effort index for vessel i, $(HP)_i$ = horsepower for vessel i, $(LFR)_i$ = sum of the lengths of the footropes measured in yards for vessel i, (38) = average horsepower of the smallest class of vessels operating in the Gulf from 1962 to 1971, and 14.6 = average net size measured in yards of footrope used by the smallest class of vessels for the same period [Griffin, W. L., M. L. Cross, R. D. Lacewell, and J. P. Nichols. 1973. Effort index for vessels in the Gulf of Mexico shrimp fleet. (Unpubl. rep. to NMFS, contract no. 03-3-042-19 with the Tex. Agric. Exp. Stn., Tex. A&M Univ.].

vessels in 1973 prices. Depreciation charges were calculated using the straight-line method, based on the estimated 1973 replacement value for each vessel, and using an 8-yr depreciable life with 35% book salvage value. For the amortization schedule, the same 1973 equivalent new vessel costs were used, with 67% of the cost financed at a 9% interest rate, for 8 yr, and with 12 equally amortized payments per year. These terms were found to be representative for 1973 through interviews with officers of financial institutions which engage in shrimp vessel financing. The specific amount of interest reported in each costs and returns budget is for the fifth year of the amortization schedule since the majority of the vessels in the sample taken were from 3 to 6 yr old.

Required return to equity capital is economic rather than financial in concept and is an attempt to place a value on the opportunity cost of the equity capital committed to an investment. At the time an owner invests in a shrimp vessel he has several alternative investments available with various rates of return associated with each. Theoretically these different rates of return are representative of the relative risks associated with each—that is, risk and return vary directly. Because the alternative investment opportunities are different for each owner, in the interests of standardization the rate of interest charged by financial institutions for shrimp vessel financing (9%) was assumed to be the highest alternative rate available to the owners for an investment of equivalent risk and can be adjusted by an individual owner to reflect his own investment alternatives.

A note of explanation is necessary concerning the cash flow budgets and cash flow analysis. Terminal vessel value (sale value) and holding period were established by asking each vessel owner to estimate, in 1973 dollars, what that same vessel would be worth as a used vessel if he had held it for the number of years that he customarily fishes a new vessel. Respondents indicated they fished a new vessel from 3 to 15 yr, with 8 yr being the most frequent response, and that even in periods of relative price stability an 8-yr-old shrimp vessel is worth approximately 65% of its original cost. Furthermore, that difference between the 35% book value for depreciation purposes and the 65% terminal value is evidenced by the frequency of income taxes levied on vessel owners for depreciation recapture at the time of replacement. For those reasons, an 8-yr holding period and a 65% terminal value were used in the cash flow budgets.

RESULTS

Classification of Vessels

Vessels were grouped according to construction, keel length, and effort index (Table 1). All vessels in the sample were either wood or steel. Vessels were divided into three keel length intervals: 45-62 feet, 63-69 feet, and 78-80 feet. The range of effort indices was divided into three intervals: 1.64-1.89 units, 1.90-2.19 units, and 2.20-2.51 units. Using these groupings for classification, 12 combinations were possible and the vessels in the sample fell into 9 of those possible combinations (See Appendix).

Predicted average cost values for the 115 vessels were plotted and vessels were classed into five general categories as shown in Table 1, where class I is the highest cost curve and class V is the lowest. Classes I and II, the two highest cost curves, consist entirely of steel vessels whereas classes III, IV, and V consist entirely of wooden vessels. The position of the average cost curves seem to be related to vessel length for each type construction except for class IV which includes two length intervals.

These results are not surprising. Previous research by Nichols and Griffin (1974) indicated that smaller, less powerful wooden vessels can produce a given quantity of shrimp at a lower cost than can a larger, more powerful steel vessel. As a matter of fact, their research showed that a 50% reduction in total effort exerted by the shrimp fleet would only reduce total catch by about 10%.

For the 4-yr period, 1962-65, the average vessel exerted about 1.16 units of effort in a day fished

TABLE 1.—Classification of Gulf of Mexico shrimp vessels, based on construction, keel length, and effort index from a sample of 115 vessels, 1973.

Vessel class	Construction	Keel length (feet)	Effort index (units)
I	Steel	70-78	1.90-2.19
			2.20-2.51
II	Steel	63-69	1.90-2.19
			2.20-2.51
III	Wood	63-69	1.90-2.19
			2.20-2.51
IV	Wood	45-62	1.90-2.19
		63-69	1.64-1.89
V	Wood	45-62	1.64-1.89

and the annual landings per vessel were 31,700 pounds of shrimp (heads-off). However, in the 4-yr period, 1970-73, the average vessel exerted about 1.68 units of effort in a day fished and the annual landings were only 28,900 pounds (heads-off). The average length of the vessel operating in the Gulf also increased over time (Nichols and Griffin 1975). Thus, as additional effort has been added to the Gulf of Mexico shrimp fishery—by increasing the number of vessels and/or the average size of the vessel—the total pounds landed have been divided between more and more units of effort.

From these figures it is apparent that the average Gulf of Mexico shrimp vessel has been increasing in size and relative fishing power and the annual landings per vessel have declined. Due to the lower investment levels and lower operating costs of smaller, less powerful vessels it follows that those smaller vessels could produce a pound of shrimp at a lower unit cost than could a larger, more powerful vessel if both were fishing the same or equally abundant fishing grounds. However, two distinctions and/or disadvantages of the smaller vessels compared to larger vessels must be noted here. First, as discussed earlier, shrimp is not a homogeneous product, and larger shrimp command higher ex-vessel prices than do smaller shrimp. Because the larger shrimp are usually associated with deeper waters, farther out in the Gulf, a smaller vessel with less capacity both for deepwater trawling and for holding fuel and shrimp is at a disadvantage compared with a larger vessel because of that depth and distance from shore.

The second distinction, and associated with the first, is the fact that larger vessels are better able to operate in and cope with rougher seas and the frequent storms in the Gulf than are smaller vessels. Therefore, the smaller vessels would either be forced to trawl closer to shore for smaller, less valuable shrimp, or for a given period of time in the deeper fishing grounds with typical weather conditions, the smaller vessels would not be able to realize as many actual fishing hours as a larger vessel operating in the same waters during the same period of time.

Comparison of Classes

Table 2 shows a summary of the costs and returns, equity requirements, payback period, and internal rate of return for the five classes of shrimp vessels operating in the Gulf of Mexico in 1973 (a more detailed break down of cost is available from the authors). Class I vessels received the highest price per pound, $2.03, for the shrimp landed but produced 5,500 pounds less shrimp than the smaller class II vessels. Class I vessels also had the highest levels of variable costs not proportional to catch, $45,152, the highest fixed costs, $31,906, and the highest total costs, $108,291, of any of the general classes. These cost relationships were to be expected since the larger steel vessels should have the highest initial investment requirements and operating costs. Due to low production and high cost, these vessels averaged the greatest loss for the year, $20,704, and payback did not occur. The internal rate of return on investment was negative.

TABLE 2.—Summary of costs and returns information, net present value analysis, and pay back period for five classes of shrimp vessels operating in the Gulf of Mexico in 1973.

Item	Vessel class				
	I	II	III	IV	V
Number of vessels	14	28	48	15	10
Catch (pounds)	43,146	48,602	39,170	30,716	30,950
Gross revenue:					
Per pound ($)	2.03	1.89	1.93	1.65	1.55
Total ($)	87,587	91,802	75,764	50,770	48,044
Cost:					
Variable					
Not proportional to catch ($)	42,152	31,694	28,134	22,835	16,784
Total ($)	77,195	68,600	58,543	43,444	36,385
Fixed ($)	31,096	22,642	22,231	18,550	15,296
Total ($)	108,291	91,242	80,774	61,994	51,681
Returns above variable cost ($)	10,392	23,202	17,221	7,326	11,659
Net revenue ($)	-20,704	560	-5,010	-11,224	-3,637
Equity requirement ($)	47,407	38,921	30,630	24,200	22,176
Payback period (yr)	[1]	[2]	[2]	[1]	[2]
Internal rate of return (%)	[3]	13.21	2.65	[3]	2.63

[1]Does not occur.
[2]Does not occur through operations—payback in the eighth year is due to sale of the vessel.
[3]Less than 0%.

Class II vessels had the highest landings, 48,602 pounds, of the five classes of vessels. They also had the highest gross revenues even though the average price per pound received was $0.14 less than class I vessels. They did experience relatively high total costs, yet the variable costs not proportional to catch, the "manageable" variable costs, were $10,500 less than class I. Class II vessels were able to register a positive return to owner's labor and management of $560—the only one of the classes to achieve that. Payback occurred only with the sale of the vessel in the eighth year. The internal rate of return on investment was 13.21%, which was the highest of the five classes.

Class III was the most populous class. Gross revenue was approximately $15,000 below and total costs were about $10,500 below those of class II vessels. The difference in the total costs was due to costs directly proportional to catch—a reflection of the fact that class III vessels caught roughly 9,000 pounds less shrimp than did the class II vessels. Class III vessels had a negative net return of $5,010. The internal rate of return on investment was 2.65% and payback occurred during the eighth year only with the sale of the vessel.

Class IV vessel production was about 9,000 pounds less than class III vessels and the price per pound was about $0.30 less, so that gross revenue was $25,000 lower for the class IV vessels. Variable costs not directly proportional to catch were roughly $5,000 lower, and total cost was $19,000 less for class IV vessels than for class III vessels. Because of the low level of production and gross revenues, class IV vessels had the second greatest net loss, $11,224, of any of the five classes, and payback did not occur. The internal rate of return on investment was negative.

Class V vessels reached roughly the same level of production as did class IV vessels, but at $6,000 lower variable costs not directly proportional to catch. Comparison of the returns above variable costs shows class V vessels contributed over $4,000 more towards fixed costs than did class IV, while receiving some $2,000 less in gross revenues. Net revenue was a negative $3,637, but was still the second highest with respect to the other four classes. Payback occurred in year 8 only with the sale of the vessel and the internal rate of return on investment was 2.63%.

Financial Analysis with Cost Adjusted to 1974 and 1975

Fishing for shrimp in the Gulf of Mexico in 1973 was definitely not an enterprise in which profits could be achieved across the board. Figure 1 shows the break-even undiscounted cash flow analysis for each of the five vessel classes, based on 1973 costs and for costs updated to 1974 and 1975. Costs for 1974 were calculated by increasing all cost items (fixed and variable) by 20%[5] except fuel and new vessel cost. Because fuel represents such a large portion of a vessel's operating costs, it was treated separately and increased from 18 to 32 cents per gallon. New vessel cost was held constant at 1973 levels since there has not been a significant number of vessels entering the industry since 1973. Inflation is expected to continue to increase at a rate between 5 and 15%; therefore, 1975 costs were increased by 10% over 1974 levels with the exception of new vessel prices. For comparison purposes the vertical dashed lines, labeled 1973, indicate the 1973 average landings and the horizontal dashed lines indicate the 1973 average ex-vessel price received for each vessel class.

1974 Analysis

Input prices continued their upward trends in 1974. At the same time landings showed approximately a 2% improvement over the 1973 levels, but shrimp prices fell by approximately 20%; the combined effect was a 15% drop in the value of shrimp produced in the Gulf of Mexico in 1974.[6] Figure 1 explains graphically the ramifications of such conditions on the undiscounted break-even cash flows for each of the five vessel classes. As the graphs show, none of the classes would have experienced a break-even cash flow for 1974 given the 20% decrease in shrimp prices and minimal increase in landings over the 1973 levels. This of course means that none would

[5]Based on the July 1974 wholesale price index including all commodities (Board of Governors of the Federal Reserve System 1974).

[6]Total Gulf of Mexico shrimp landings (heads-off) in 1973 were 114.8 million pounds, average ex-vessel price per pound received was $1.50 and the value was $171.7 million (United States Department of Commerce 1974). Landings for the same period in 1974 were 116.9 million pounds, the average ex-vessel price per pound was $1.18, and the value of the landings was $137.4 million (United States Department of Commerce 1974-75).

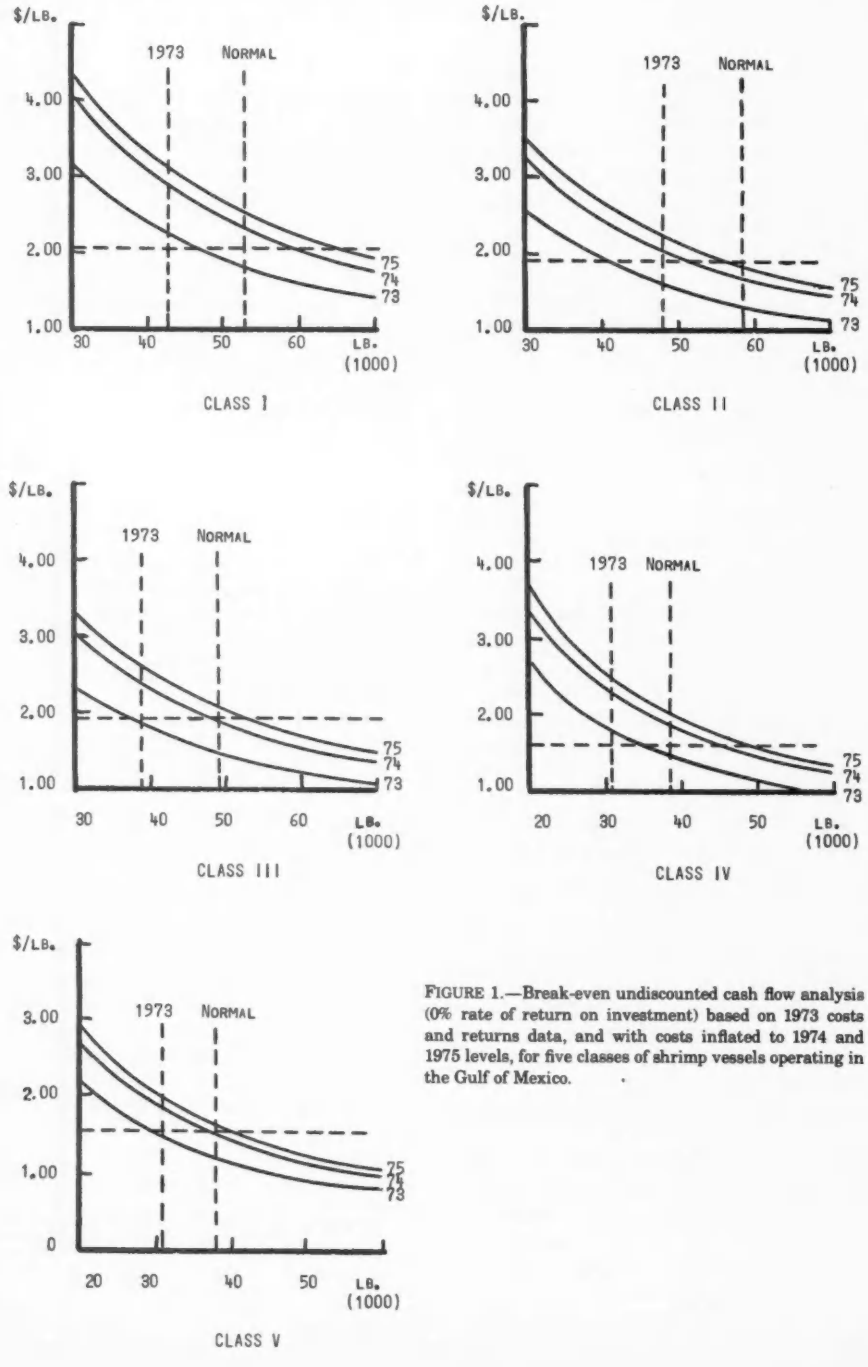

FIGURE 1.—Break-even undiscounted cash flow analysis (0% rate of return on investment) based on 1973 costs and returns data, and with costs inflated to 1974 and 1975 levels, for five classes of shrimp vessels operating in the Gulf of Mexico.

have registered a positive return on investment. As a matter of fact, the class II vessels, which had the highest rate of return in 1973, would have had to receive approximately $2.20 per pound of shrimp landed to achieve a break-even investment (0% internal return on investment) if annual production of shrimp is held constant at the 1973 level of 48,602 pounds. Since they only received $1.89 per pound in 1973 and prices declined in 1974, investment in a class II vessel in 1974 would have yielded a negative rate of return on investment.

1975 Analysis

If inflation continues at a 10% rate in 1975, and production remains at approximately the 1973 level, Figure 1 indicates that ex-vessel prices would have to increase to approximately $3.10, $2.25, $2.65, $2.50, and $2.00 per pound of shrimp landed for vessel classes I, II, III, IV, and V, respectively, to achieve even a zero internal rate of return on investment. Or, on the other hand, with prices remaining constant at the 1973 level, production would have to increase to approximately 66,000, 57,000, 52,000, 49,000, and 40,000 pounds of shrimp landed per vessel, respectively.

However, based on production functions estimated by Nichols and Griffin (1974) for the Gulf of Mexico shrimp fleet where catch is a function of effort, 1973 production of shrimp from the Gulf was below normal. Average annual landings for the vessels in the sample were estimated in a normal year to be approximately 53,000, 59,000, 49,000, 37,000, and 38,000 pounds of shrimp landed per vessel for classes I, II, III, IV, and V, in that order. The vertical dashed lines in Figure 1 labeled "normal" indicate the average landings for each class of vessel for the normal production year.

The average vessel in class II seems to be operating at better than a break-even level in 1975 assuming normal production and 1973 ex-vessel prices for shrimp. That is, given normal production, class II vessels would have to receive $1.85 per pound for shrimp landed in 1975 while the 1973 average price for the class was $1.89 per pound. But, a new vessel cost of $130,000 would be just enough to set this cash flow at the break-even level and the replacement of a class II type vessel is estimated to be in excess of $150,000 in 1975.

From the graphs in Figure 1 it is obvious that none of the other classes (I, III, IV, V) are operating at the break-even level assuming a normal production year and 1973 average shrimp prices and new vessel costs. In order to bring the cash outflows down to the levels necessary to achieve break even, class III-type vessel owners could only invest approximately $30,000 in a new vessel in 1975, and class V owners could invest no more than $40,000. To reiterate, these break-even levels represent a zero internal rate of return on investment. Significantly, class I and class IV-type vessel owners could not achieve the breakeven level even with a zero investment requirement.

DISCUSSION AND IMPLICATIONS

The resolution of problems facing the Gulf shrimp industry may come about as a result of changing economic conditions and/or changes in specific policies which may or may not be initiated or suggested by the industry. A number of possible changes have been suggested which bear consideration.

One suggestion has been a fuel subsidy for the fishing industry. This would be a direct saving to vessel owners on the largest single input cost item. Assuming a normal production year, it would take a subsidy of 35, 13, 48, and 15 cents per gallon for classes I, III, IV, and V, respectively, to break even with a zero return on investment assuming prices stayed constant at the 1973 level. Chances of obtaining any relief in this area are very slim. At best, the extent of such relief would likely be limited to future increases related to oil import taxes. Current fuel expenses would probably not be reduced.

Efforts to improve the efficiency of fishing operations are also a priority consideration. The operation of fishing vessels during periods of marginal profitability required improved management and closer consideration of the effects of the day-to-day decisions in running the vessel.

Import quotas and tariffs are one suggested alternative to the current cost-price squeeze in the industry. By controlling imports it is anticipated that supplies on the market can be reduced thus preventing prices from being depressed below the domestic producer's costs. The goals of free trade and stabilized or lower consumer prices may make approval of the necessary controls through the political process difficult to realize.

Market expansion and development programs have also been suggested as a means of shifting demand and increasing prices. Market development is a long term process and the industry should commit itself to such a program. This suggests a greater continuity of programs than the occasional reaction to crisis situations which are evident in the recent history of the industry.

A much larger question has been introduced in this discussion of economic efficiency. Industry sources have indicated a concern that the industry has become overcapitalized in shrimp trawling vessels. One classic solution to this is a total fisheries management scheme which includes a limited entry concept. Other conditions assumed equal, this would increase catch per unit of effort and would result in lower costs per unit of shrimp landed. This is not a short-run solution, however. It is only now being experimented with in U.S. fisheries. A great deal of planning and information would be needed to design and implement such a program.

Long-run problems of limited entry include the possibility of creating a stagnant, protected industry which loses touch with both the consumer market and the market for resources. In the long-run this may be more detrimental than going through periodic readjustments such as that which the industry currently faces.

If it can be assumed that the relative positions of the unit cost and revenue curves remain constant in the future and assume normal production years, then based on the sample size of each vessel class, the percentage reduction in vessels needed for break even can be calculated. Using class I as an example, in a normal year, the 14 vessels in class I would have landed a total of 742,000 pounds of shrimp. To experience a break-even rate of return, each vessel would have to land 66,000 pounds of shrimp. Dividing 66,000 pounds per vessel into 742,000 pounds implies that class I's total production of 742,000 pounds could only support approximately 11 vessels or 79% of the vessels sampled.[7]

CONCLUSIONS

The major conclusion from the analysis presented here is that investment in a shrimp trawler is unprofitable assuming the environment existing in 1973 when these data were collected and for which the average relationships were estimated. The analysis permits tracing the effects of altered assumptions regarding average prices and vessel landings on profitability. Only class II vessels showed profits under the 1973 conditions.

The shrimp industry is undergoing considerable economic stress. The underlying causes relate to factors in the general economy beyond industry control and the rapid expansion in potential fishing effort which occurred during the period since the late 1960's. Means of coping with this stress include both improved management to reduce costs and various forms of government programs will be necessary to permit the implementation of some of these ideas.

Perhaps some would prefer to allow a period of significant readjustment forcing the marginal firms to leave the industry. The costs of this readjustment, both economic and social, must be considered by those who propose this solution. Several things could happen which would prevent a significant readjustment: landings could increase dramatically, the economy could recover quickly thus improving demand and prices, or input costs could decline. However, these things may not happen soon enough to avoid the difficult readjustment problems.

[7]It is obvious that if the total Gulf shrimp fleet were reduced to 79% of its current size, total production would also decrease. That is, the estimated reduction in the fleet should be adjusted with respect to the production function. However, calculations using the production function made less than a 1% difference.

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APPENDIX

Average cost equations were estimated using ordinary least squares regression analysis for each of the nine groups of vessels by the use of linear, quadratic, and log linear functions. In general, considering all nine equations, the log linear model gave the best statistical results whereas the quadratic gave the worse. This implies that the average cost curves were ever decreasing over the range of the data available. Predicted values from the log linear model for the nine equations were plotted by the computer on one graph and compared. Because all nine plots were relatively parallel, economies of scale did not exist over the range of the sampled data.

Since the plotted predicted values were relatively parallel, one average cost equation was estimated using construction, length, and effort as dummy variables. All three were statistically significant variables at least at the 95% level of confidence in explaining the average costs of producing shrimp. For a more detailed discussion see Wardlaw and Griffin (1974).

LONG-TERM FLUCTUATIONS OF EPIBENTHIC FISH AND INVERTEBRATE POPULATIONS IN APALACHICOLA BAY, FLORIDA

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ABSTRACT

A 3-yr study was made concerning seasonal changes in the biota of Apalachicola Bay. The Apalachicola River causes a temporal progression of changes of various environmental parameters in the bay such as salinity, turbidity, nutrients, and detritus levels. Fishes were more widespread in their distribution throughout the bay than invertebrates. This was thought to be related to trophic response and habitat preference. High levels of relative dominance prevailed for both groups with the top three species of each group accounting for more than 80% of the total number of individuals taken.

Peak levels of monthly abundance of various dominant fish species tended not to overlap through a given 12-mo period. Invertebrate species abundance usually reached peak levels during summer and fall periods. The seasonal appearance and distribution of organisms in the Apalachicola Bay system was comparable to that found in other estuaries in the northern Gulf of Mexico. The temporal and spatial distribution of estuarine fishes and invertebrates was associated with species-specific reproductive cycles, trophic relationships, and habitat preferences. The Apalachicola estuary was viewed as a seasonally stable system, with regular temporal fluctuations of the biota through each annual cycle.

There is a rapidly growing literature concerning fluctuations of populations of epibenthic estuarine organisms (Dahlberg and Odum 1970; Bechtel and Copeland 1970; Copeland and Bechtel 1971; McErlean et al. 1973; Oviatt and Nixon 1973; Copeland and Bechtel 1974; Gallaway and Strawn 1974; Livingston 1975). Haedrich and Haedrich (1974) noted that seasonal changes of fish populations in a Massachusetts estuary allow more species to utilize the estuary than if there were constant direct competition. Staggered reproductive cycles were postulated as a partial explanation for this "dynamic situation." Trophic variability was also considered a mechanism for reduced competition. Copeland and Bechtel (1974) identified key environmental requirements for six Gulf coast species, and considered such limits as potential criteria for estuarine management programs. Oviatt and Nixon (1973) noted that although fish biomass remained constant throughout the year, individual species abundance varied seasonally. They found that biomass and numbers of individuals could not be accounted for on the basis of physical parameters alone, and it was considered that biological functions such as competition and predation could be more important determinants of species distribution in estuarine systems.

The present study is part of a comprehensive field program in Apalachicola Bay, Fla. (Livingston et al. 1974). This is a relatively unpolluted, shallow coastal estuary bounded by barrier islands. The bay is physically dominated by the Apalachicola River (Estabrook 1973; Livingston et al. 1974). This paper is concerned with long-term, seasonal fluctuations of epibenthic fish and invertebrate populations, and the possible interrelationships of the physicochemical and biological elements of the Apalachicola Bay system.

MATERIALS AND METHODS

Field Operations

A detailed description of the sampling methodology is already available (Estabrook 1973; Livingston et al. 1974). Physicochemical and biological samples were taken monthly from March 1972 to February 1975 at a series of stations in East Bay and Apalachicola Bay (Figure 1). Water samples were taken at the surface and

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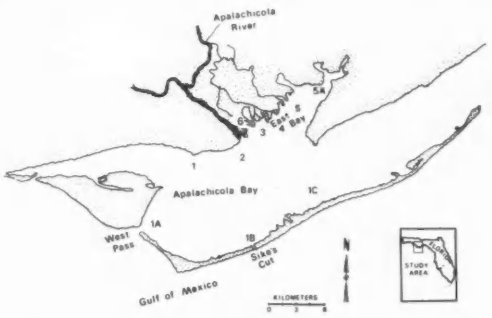

FIGURE 1.—The Apalachicola Bay system with permanent sampling stations for long-term studies concerning fluctuations of populations of epibenthic fishes and invertebrates.

bottom with a 1-liter Kemmerer bottle. Temperature was measured with a stick thermometer and/or a YSI[2] dissolved oxygen meter. Salinity was determined with a temperature-compensated refractometer periodically calibrated with standard seawater. Color was measured with a (Hach) American Public Health Association platinum-cobalt standard test while turbidity was determined with a Hach model 2100A turbidimeter. Light penetration readings were taken with a standard Secchi disk. River flow data were provided by the U.S. Army Corps of Engineers (Mobile, Ala.) while local climatological information was provided by the Environmental Data Service, NOAA, U.S. Department of Commerce.

Biological collections were made with 5-m (16-foot) otter trawls (¾-inch mesh wing and body; ¼-inch mesh liner). Repetitive, 2-min trawl tows were taken at each station at speeds of 2-3 knots. Seven subsamples were taken at stations 1, 2, 4, 5, and 6 while two samples were taken at stations 1A, 1B, 1C, 3, and 5A. All organisms were preserved in 10% Formalin, sorted and identified to species, measured and/or counted (standard length for fishes; total length for shrimps; carapace width for blue crab, *Callinectes sapidus*). Stations 1 and 4 were also sampled at night, approximately 1-2 h after sunset for the first 2 yr of the study.

All statistical analysis was carried out using an interactive computer program designed for the study of extensive data collections. The extent of interstation community similarity was tested using the C_λ index of overlap (Morisita 1959; Horn 1966). This index determines the probability that two randomly drawn samples from populations X and Y will be the same species relative to the probability that two individuals of the same species will be drawn from population X or Y alone.

$$\lambda_x = \frac{\sum_{i=1}^{S} x_i^2}{X^2} \qquad \lambda_y = \frac{\sum_{i=1}^{S} y_i^2}{Y^2}$$

$$C_\lambda = \frac{2\sum_{i=1}^{S} x_i y_i}{(\lambda_x + \lambda_y)\,XY}$$

where S = number of species

x_i and y_i = number of individuals of the ith species in populations X and Y

X and Y = total number of individuals in the two communities

λ_x and λ_y = measures of diversity (Simpson 1949) as modified for sampling with replacement (Horn 1966).

Values for this index range from 0 (no species in common) to 1. A hierarchical (stepwise) multiple regression analysis was carried out using monthly population size as the dependent variable. Various physicochemical and biological parameters (temperature, salinity, chlorophyll *a*, turbidity, color, Secchi disk depth, total depth, local rainfall, wind speed and direction, tidal stage, river flow, and dissolved oxygen) were used as the independent variables. All such functions were tested in the same month of collection and with a 1-mo lag in the physicochemical parameters. Due to the relatively high number of independent variables, the stepwise regression was used whereby one variable at a time was systematically introduced into the equation, and, at each step, the variable added was the one giving the greatest increase in the multiple correlation coefficient. While not necessarily giving the "best" equation, this method is computationally feasible, and frequently gives results comparable to methods that would determine all possible regressions. Since the salinity, color, and turbidity

[2]Yellow Springs Instrument Co. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

data had skewed distributions, logarithmic transformations were used for such variables to approximate normality.

RESULTS

Physicochemical Parameters

Depths of the various stations ranged from 1 to 2.5 m. With the exception of shallow areas, such as station 6, which are characterized by periodically moderate concentrations of widgeon grass, *Ruppia maritima*, East Bay has a silty-sand bottom with little benthic macrophyte development. Stations proximal to river drainage (stations 2-4) are marked by strong currents and seasonally high deposits of allochthonous detritus (leaf litter, branches, etc.). Except for shallow fringing areas, Apalachiocola Bay (stations 1, 1A-1C) has little benthic macrophyte development; it is dominated by silty-sand bottom with interspersed oyster bars.

The Apalachicola River is a major determinant of the physical environment of the bay system. There is a seasonal fluctuation in flow with peak levels occurring during winter and spring months. Local rainfall, with peaks during late summer and early fall, is out of phase with this pattern. During the present period of study, river flow determined salinity throughout the bay. Mean salinity in East Bay was lower than that in Apalachicola Bay; oligohaline areas (stations 5A, 6) were without measureable salinity from midwinter to early summer. Outer bay stations had higher salinities; at station 1B, the salinity did not go below 15‰ during the 3-yr study. During periods of increased salinity, the shallow bay system was vertically stratified (Estabrook 1973; Livingston et al. 1974). However, there was little horizontal or vertical variability in water temperature at any given time. Low temperatures occurred during the winter months. Turbidity levels were relatively high throughout the bay, and were directly related to river flow rates. Color levels reflected both river flow and proximity to land runoff, with elevated levels in East Bay areas during the summer. Although there were various complex physical changes in different areas of the bay due to basin physiography, local runoff, tidal currents, depth, etc., the major habitat features of the Apalachicola Bay system were determined by river conditions.

Distribution of Fishes and Invertebrates

Similarity coefficients (cumulative, by station) are shown in Table 1. Species such as bay anchovy, *Anchoa mitchilli*; Atlantic croaker, *Micropogon undulatus*; and sand seatrout, *Cynoscion arenarius*, were dominant throughout the sampling area. Others such as scaled sardine, *Harengula pensacolae*, and Gulf menhaden, *Brevoortia patronus*, were taken primarily in East Bay. High interstation similarity of species assemblages of fishes was noted, although grass bed areas such as station 6 were characterized by higher numbers of species than other (mud-flat) stations. There was increased spatial variability among the invertebrate assemblages. Species such as the blue crab and the penaeid shrimps (*Penaeus setiferus*, *P. duorarum*) were more evenly distributed throughout the system than others. Grass shrimps (*Palaemonetes pugio*, *P. vulgaris*, *P. intermedius*) were more frequently taken in the grass beds of East Bay while the brief squid, *Lolliguncula brevis*, was a dominant species in Apalachicola Bay. High levels of species similar-

TABLE 1.—C_λ values (by station) for invertebrates and fishes taken in the Apalachicola Bay system (March 1972-February 1975).

Station		Station 1 Day	Station 1 Night	1A	1B	1C	2	3	4 Day	4 Night	5	5A	6
							Fishes						
1 day			0.96	0.94	0.79	0.95	0.97	0.80	0.92	0.99	0.94	0.95	0.93
night		0.63		0.76	0.52	0.95	0.87	0.58	0.77	0.95	0.79	0.83	0.85
1A		0.85	0.54		0.93	0.84	0.95	0.93	0.96	0.69	0.96	0.97	0.80
1B		0.36	0.29	0.22		0.65	0.84	0.94	0.88	0.73	0.98	0.87	0.91
1C		0.57	0.46	0.86	0.91		0.94	0.67	0.84	0.95	0.89	0.90	0.78
2		0.82	0.34	0.58	0.22	0.23		0.85	0.94	0.98	0.95	0.97	0.94
3		0.68	0.53	0.50	0.15	0.31	0.49		0.95	0.78	0.95	0.91	0.84
4 day		0.96	0.54	0.73	0.20	0.38	0.92	0.68		0.91	0.99	0.98	0.92
night		0.87	0.90	0.69	0.24	0.69	0.62	0.69	0.82		0.93	0.94	0.93
5		0.74	0.25	0.53	0.10	0.19	0.98	0.41	0.85	0.50		0.98	0.92
5A		0.84	0.36	0.58	0.09	0.58	0.97	0.54	0.94	0.64	0.97		0.96
6		0.23	0.20	0.16	0.06	0.09	0.16	0.79	0.28	0.25	0.17	0.21	
	Invertebrates												

ity were noted among river-dominated and East Bay stations (1, 2, 4, 5, 5A); outer bay stations (1A, 1B, 1C) also were somewhat alike according to the C_λ similarity analysis. Station 6, as a grass-bed area, differed from most of the other collections. Station 1B, with consistently higher salinity than the other stations, differed in terms of invertebrate species composition. These data indicate that fishes are more widespread in their distribution throughout the bay system than the invertebrates, which were more habitat-specific with respect to substrate, salinity, etc.

Seasonal Fluctuations of Dominant Species

Comparative dominance figures for the 10 most numerous fish and invertebrate species are given in Table 2. Relative dominance is high in both groups with the top three species of fishes and invertebrates constituting 77.0 and 80.7% of the respective combined totals. Some species such as *H. pensacolae*, *B. patronus*, and Atlantic threadfin, *Polydactylus octonemus*, were found during limited periods (April 1973, April 1974, and May-August 1973, respectively). Seasonal variations in the six dominant species are shown in Figure 2. The most conspicuous species was *A. mitchilli*, which was particularly abundant during the first year of study. Peaks of numbers usually occurred during fall or early winter (October-January). With *M. undulatus*, peak levels usually were noted during late winter or early spring (February-March) whereas *C. arenarius* reached abundance during late spring and summer months (usually around August). The sea catfish, *Arius felis*, usually peaked by midsummer (July) while Atlantic bumper, *Chloroscombrus chrysurus*, and southern kingfish, *Menticirrhus americanus*, were prevalent during late summer or early fall (August-October). The spot, *Leiostomus xanthurus*, usually peaked during winter and spring months; silver perch, *Bairdiella chrysura*, had a variable abundance curve. Overall, there was considerable regularity in the appearance of the dominant bay fishes even though there was often a marked within-species variation in total numbers from year to year.

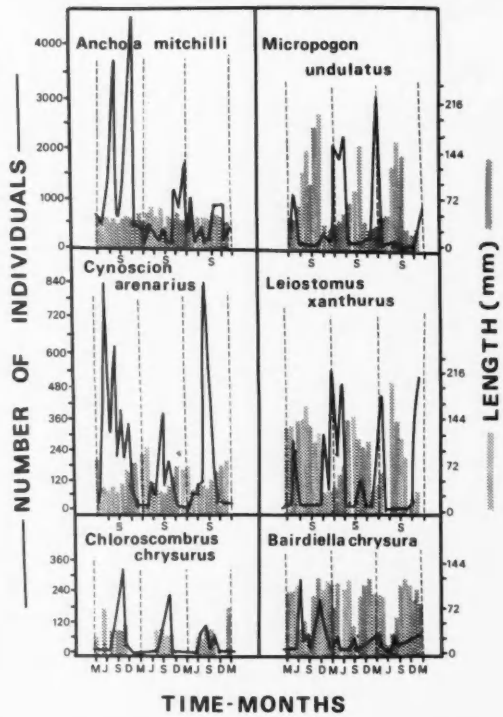

FIGURE 2.—Seasonal changes of numbers of individuals and mean size of six dominant species of fishes taken in the Apalachicola Bay system from March 1972 to February 1975.

TABLE 2.—The 10 dominant species of fishes and invertebrates taken in the Apalachicola Bay system from March 1972 to February 1975. Figures are expressed in percentages of total numbers of individuals.

Fish	%	Invertebrate	%
Anchoa mitchilli	42.3	*Penaeus setiferus*	40.1
Micropogon undulatus	26.0	*Palaemonetes pugio*	20.4
Cynoscion arenarius	8.7	*Callinectes sapidus*	20.2
Leiostomus xanthurus	5.4	*Penaeus duorarum*	5.3
Harengula pensacolae	2.6	*Lolliguncula brevis*	4.3
Bairdiella chrysura	1.6	*Penaeus aztecus*	2.6
Chloroscombrus chrysurus	1.5	*Neritina reclivata*	1.5
Polydactylus octonemus	1.4	*Portunus gibbesii*	1.1
Arius felis	1.3	*Palaemonetes vulgaris*	0.8
Brevoortia patronus	1.2	*Rhithropanopeus harrisii*	0.5

Annual fluctuations of the dominant invertebrate species are shown in Figure 3. The white shrimp, *Penaeus setiferus*, was prevalent from August to November with autumn peaks of abundance; the other penaeids usually reached high numbers in the late spring (*P. aztecus*) or late summer (*P. duorarum*). *Palaemonetes pugio* was usually found in the bay during spring months (March-May) while *P. vulgaris* reached high numbers in November. The blue crab peaked during summer and winter periods. Early summer and fall peaks were noted for *Lolliguncula*

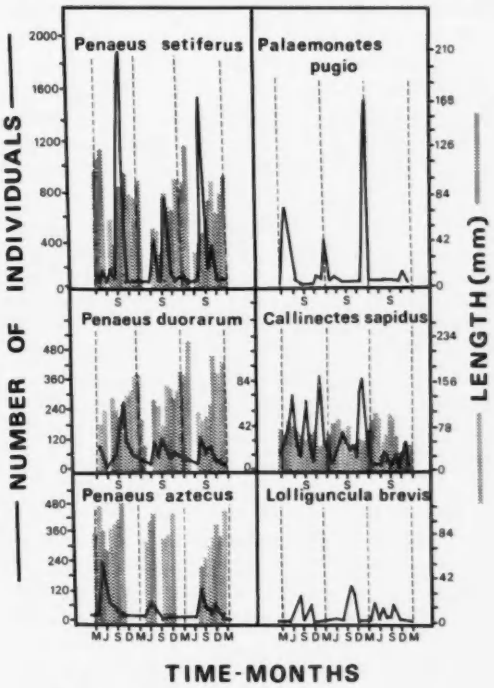

FIGURE 3.—Seasonal changes of numbers of individuals and mean size of six dominant species of invertebrates taken in the Apalachicola Bay system from March 1972 to February 1975 (*Palaemonetes pugio* and *Lolliguncula brevis* were not measured).

brevis. Unlike the fishes which usually reached peak levels during different months of the year, the invertebrates tended to increase in numbers during spring and fall periods.

Annual peaks of abundance often coincided with influxes of juvenile fishes and invertebrates. A more detailed analysis of this is shown for two representative species of fishes (Figure 4) and invertebrates (Figure 5). The young stages of *Micropogon undulatus* entered the bay during the winter at which time there was a continuous recruitment for several months. Decreased numbers coincided with gradual increases in size during spring and summer months. With *Cynoscion arenarius*, recruitment of young occurred during spring and summer, with subsequent increases in size during fall and winter months. The blue crab had peaks of young individuals during summer and winter periods although an almost continuous succession of young crabs entered the bay during the year. Young stages of *Penaeus setiferus* were found during the summer with growth occurring through fall and winter. The other penaeid shrimps had similar growth patterns with recruitment of the young during summer and fall periods. The data indicate that various patterns of recruitment and growth occur among the different estuarine species, although the inverse relationship of numbers and size appears to hold for most of the dominants.

Results of the regression analysis are shown in Table 3. Factors such as chlorophyll *a*, Secchi disk readings, and color repeatedly accounted for some of the variability associated with fluctuations of estuarine populations. Often such associations were made with a 1-mo lag in the independent variable. In most cases, the given independent variables accounted for less than 50% of the variability of the population data. There was a distinct correlation with factors related to trophic phenomena such as chlorophyll *a* and Secchi disk readings; this would indicate that biological functions such as feeding behavior and reproduction could play an important role in the determination of population shifts in the Apalachicola Bay system. These data indicate that no single set of forcing functions can account for the population changes of various estuarine species. Species abundance is dependent on complexes of interactions and possibly can be accounted for more adequately by relating such processes to dynamic changes in physical variables as well as important biological parameters. It is obvious that regression analysis cannot account for changes in

TABLE 3.—Results of the stepwise regression analysis of various independent parameters and species (population) occurrence in the Apalachicola Bay system from March 1972 to February 1975. Independent variables are listed by order of importance with R^2 expressed as a cumulative function of the given parameters.

Species	Independent variables	R^2
Anchoa mitchilli	Chlorophyll *a*, Secchi	0.38
Micropogon undulatus	River flow (lag), Secchi (lag)	0.46
Cynoscion arenarius	Chlorophyll *a*, wind, Secchi (lag), temp	0.83
Polydactylus octonemus	Chlorophyll *a* (lag), salinity, Secchi	0.58
Arius felis	Temp, wind	0.30
Leiostomus xanthurus	Turbidity (lag), Secchi, salinity, temp	0.85
Chloroscombrus chrysurus	Temp (lag), temp, salinity	0.44
Menticirrhus americanus	Temp (lag)	0.19
Symphurus plagiusa	Color (lag), color, Secchi	0.63
Bairdiella chrysura	Wind, temp, color	0.40
Peneaus setiferus	Wind, chlorophyll *a*, incoming tide, color	0.48
Palaemonetes pugio	Turbidity	0.36
Callinectes sapidus	Secchi, incoming tide	0.49
Penaeus duorarum	Chlorophyll *a*, Secchi	0.41
Lolliguncula brevis	Chlorophyll *a* (lag), temp	0.43
Portunus gibbesii	Chlorophyll *a* (lag), Secchi	0.39
Palaemonetes vulgaris	Turbidity	0.32
Rhithropanopeus harrisii	Wind	0.18
Callinectes similis	Chlorophyll *a*, temp	0.34

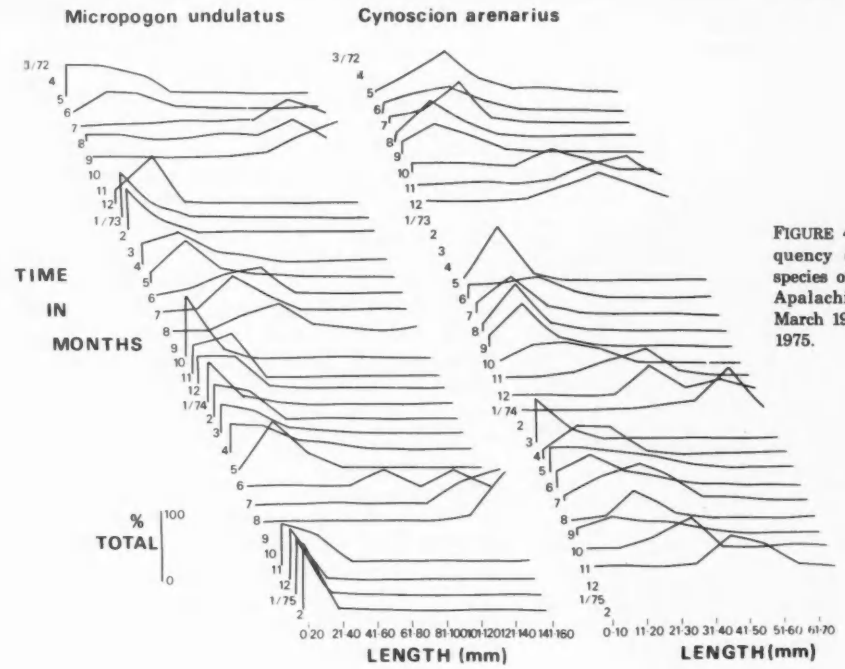

FIGURE 4.—Monthly size-frequency distribution of two species of fishes taken in the Apalachicola estuary from March 1972 through February 1975.

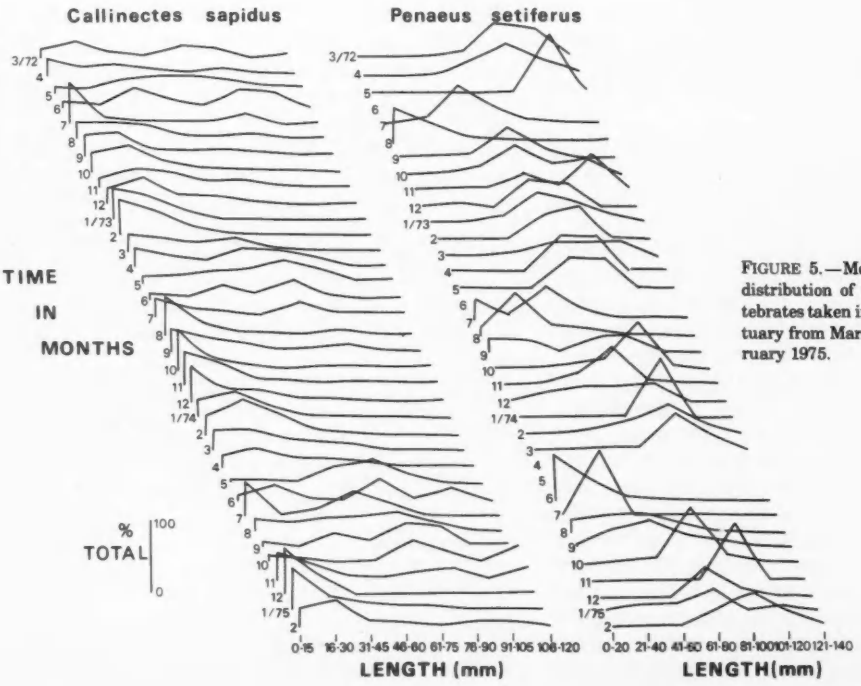

FIGURE 5.—Monthly size-frequency distribution of two species of invertebrates taken in the Apalachicola estuary from March 1972 through February 1975.

the adaptive response of populations to the extremely complex environment of the estuary. The data indicate that, in this case, temperature and salinity might not be as critical in the determination of seasonal fluctuations of estuarine populations as biological functions such as trophic response and possibly reproduction.

DISCUSSION

A review of the literature (Gunter 1945, 1950; Daugherty 1952; Reid 1955; Van Engel 1958; Gunter and Hall 1965; Williams 1965; Tagatz 1968; More 1969; Pérez Farfante 1969; King 1971; Lyons et al. 1971; Swingle 1971; Perret and Caillouet 1974; Stokes 1974; Swingle and Bland 1974) confirms that although minor variations were evident (notably among the fishes), there was a generally high level of conformity concerning the time of appearance of various dominants in the Apalachicola estuary with previously recorded data from other northern Gulf areas. Although such timing was essentially stable from year to year, there was considerable within-species variability in annual abundance. For example, the bay anchovy was particularly dominant during the summer and fall of 1972, while fewer individuals were taken during the succeeding 2 yr. The Atlantic bumper, although not considered a common Gulf species (Perret and Caillouet 1974), was relatively common in the Apalachicola estuary, especially during the first year of collection. Some species reflected particular habitat preferences: *Palaemonetes pugio* was located primarily in grass-bed areas of East Bay during periods of low salinity while *L. brevis* was found in outer bay areas during summer and fall periods of increased salinity. Although generalized temperature and salinity preferences have been shown for various estuarine species (Copeland and Bechtel 1974), as a whole these organisms show a wide tolerance for short-term changes in these parameters. This could help to explain the general lack of importance of temperature and salinity as critical variables in the multiple regression analysis; quite obviously, other functions such as acclimatization would tend to complicate such a direct approach to determination of causative agents. The multiple regression technique was limited in its application to causal relationships since various biological functions are probably involved in the determination of a given population curve.

It is possible that trophic relationships and reproductive cycles are of critical importance in the spatial and temporal distribution of estuarine populations. As in other Gulf estuaries, the Apalachicola Bay system is dominated by juvenile stages of a small number of species. The bay anchovy, abundant in a size range of 35-50 mm, is considered to be a generalized zooplanktivore at this stage, feeding in the water column on copepods, amphipods, mysids, larval and juvenile shrimps and fishes, etc. (Darnell 1958; Odum and Heald 1972; Carr and Adams 1973). Various studies (Roelofs 1954; Darnell 1958; Fontenot and Rogillio 1970) indicate that *M. undulatus* (juveniles, 10-50 mm) feeds primarily on zooplankton (copepods and amphipods) while *C. arenarius* (juveniles, 40-99 mm) consumes larger zooplanktors such as mysids, shrimp, and larval or juvenile fishes (Darnell 1958; Springer and Woodburn 1960). Juvenile (up to 40 mm) spot also feed on zooplankton; more mature fish of this species (40-200 mm) become benthic omnivores (Roelofs 1954; Darnell 1958; Springer and Woodburn 1960). Juvenile *B. chrysura* (16-160 mm) feed on copepods, mysids, shrimp, and small fishes (Darnell 1958; Carr and Adams 1973). Thus, the dominant fishes in the Apalachicola Bay system are primarily planktivorous although possible differences could exist in vertical feeding distribution and the size and species composition of the prey organisms. Previous work has shown that *Anchoa mitchilli* feeds on small crustaceans and *C. arenarius* eats the larger, more motile crustaceans. Both *Leiostomus xanthurus* and *B. chrysura* feed on small mid-water planktors (mainly copepods) as early juveniles, with later stages becoming benthic omnivores feeding largely on mysids and shrimp. Increased concentrations of zooplankton occur in Apalachicola Bay during the spring and summer while palaemonetid shrimp are abundant during winter and early spring (H. L. Edmiston pers. commun.). Thus, diversity in feeding behavior would contribute to the observed vertical partitioning of prey organisms among various planktivorous species; such data are consistent with the observed distribution of fishes in Apalachicola Bay at any given period of time.

Of the six most prevalent invertebrates in the Apalachicola estuary, five are benthic omnivores and one is a probable planktivore. Juvenile blue crabs consume detritus while larger individuals (20-200 mm) are omnivorous, feeding on detritus

and plant material, mollusks, polychaetes, crustaceans, and fishes (Darnell 1959; Tagatz 1968; Odum and Heald 1972). Penaeid shrimp are also omnivores, feeding on similar forms (Williams 1965; Darnell 1958; Eldred et al. 1961; Odum and Heald 1972). *Palaemonetes pugio* feeds primarily on detritus (Adams and Angelovic 1970; Oviatt and Nixon 1973; Welch 1975). Qualitative observations indicate that *Lolliguncula brevis* is a planktivore (Dragovitch and Kelly 1967). Thus, most of the epibenthic invertebrates utilize detritus and are more closely associated with sediment type, benthic macrophyte distribution, and placement of allochthonous forms of detritus than the planktivorous fishes; this, together with certain (species-specific) temperature and salinity tolerances, could provide a partial explanation for the observed differences in the spatial distribution of the fishes and invertebrates.

Another important evolutionary mechanism for the partitioning of the energy resources of an estuary is the temporal succession of species over an annual cycle. Abundance interrelationships expressed as percentage of total catch are shown in Figure 6. There was a certain regularity of percent representation of dominant species of fishes and invertebrates in the Apalachicola system. For example, relative occurrence of *P. pugio* was high during spring months while *Penaeus setiferus* was dominant during late summer and fall. The blue crab was abundant during winter periods. Among the fishes, *C. arenarius* was dominant during the spring and summer while *A. mitchilli* (after the first year of sampling) predominated in the fall and *M. undulatus* prevailed during the late winter and spring. When a comparison was made among the 10 most dominant species of fishes for peaks of abundance, such increases were evenly distributed over a 12-mo period. However, of the top 10 species of invertebrates, most peaks of abundance occurred during fall periods (September-November) with secondary concentrations of peaks during early summer (May-June). Livingston (in press), describing patterns of species richness and diversity in Apalachicola Bay, noted that there was an annual double peak in fish and invertebrate diversity although there was far more seasonal variability in N (numbers of individuals) and S (numbers of species) among fishes than invertebrates. These data would tend to corroborate and elucidate such findings. Thus, although the top dominants in both groups showed distinct temporal sequences in relative peak abundance, there was a tendency for increased numbers of invertebrate species during summer and fall periods whereas peaks of N and S for fishes were more continuously distributed throughout the year. Major dominants for both fishes and invertebrates thus showed temporal partitioning through an annual cycle. The noted differences in temporal distributional patterns of fishes and invertebrates could be related to trophic response, with the planktivorous fishes competing for a more limited resource than the omnivorous (detritovore and omnivore) invertebrate species.

Several conclusions can be made with regard to the biotic component in the Apalachicola estuary. Various independent ecological factors operate to determine the spatial and temporal distributions of such organisms. Biological functions, as adaptive responses to the physical and trophic environment, determine such distributional patterns, allowing a somewhat orderly temporal succession of dominant forms within certain broad trophic spectra. Patterns of reproduction of various dominant estuarine species have evolved in such a way as to permit such long-term partitioning of the estuarine environment. Superimposed on this are certain in situ mechanisms whereby further resource division occurs due to vertical and horizontal distribution of the component species. This is largely determined by various microhabitat phenomena such as salinity, bottom type, currents, availability of detritus, etc. In addition, biological determinants such as intraspecific competition and predation further modify the individual component populations. Thus, no single parameter prevails in the determination of the community structure of an estuary which undergoes predictable seasonal changes even though it is a physically forced system. Although there is considerable short-term fluctuation in the numbers of individuals of various populations, the system maintains a certain temporal constancy which, according to a traditional view of such phenomena, could be termed stability. This does not mean that such a system is not in a constantly transient state; on the contrary, through various natural and unnatural mechanisms such as habitat alteration and destruction, hurricanes, etc., the various population equilibria can be shifted so that the system is no longer characterized by a stable temporal succession of energy utilization. Each population fluctuates around a certain point of equilibrium; such fluctuations are

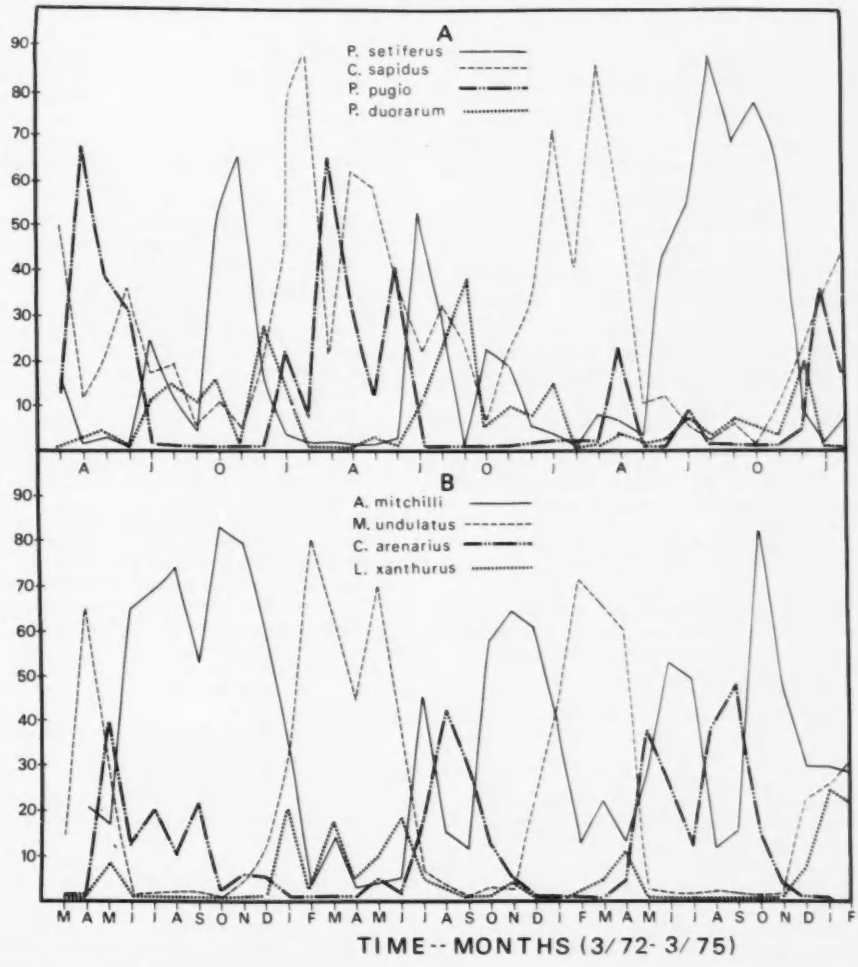

FIGURE 6.—Relative importance (% of total) of four dominant species of invertebrates and fishes taken in the Apalachicola Bay system from March 1972 through February 1975. Such species represent 82.4 and 86.0% of the respective 3-yr totals.

determined by various natural and man-induced phenomena such as overfishing and pollution. The stability of the system depends on the maintenance of various populations within certain limits of fluctuation. This has serious implications for any estuarine management program. Holling (1973) pointed out that instability (in the sense of large fluctuations) of individual populations may actually introduce a capacity for persistence or resilience. Such resilience can be attributed not only to component populations but to the system as a whole. Stability thus is seen as the "ability of a system to return to an equilibrium state after a temporary disturbance," (Holling 1973). Resilience, however, is a measure of the ability of a given system to absorb changes of primary forcing functions and still persist. By this measure, an estuarine system such as Apalachicola Bay comprises various populations which undergo considerable annual fluctuations but nevertheless are maintained within a relatively stable temporal succession.

ACKNOWLEDGMENTS

We thank Duwayne A. Meeter and Richard Gurnee for their advice concerning the statistical applications in this study. Thanks are also due to Robert C. Harriss and his staff at the Edward Ball Marine Laboratory (Florida State University) for the use of various support facilities. The authors also acknowledge Glenn C. Woodsum and J. Elton Jernigan for their help with the computer programs used in this study. Many students have also helped in the field, and are acknowledged for their interest in this project. Much of the field collections was funded by grants from NOAA Office of Sea Grant, U.S. Department of Commerce (Grant Number 04-3-158-43), and the Board of County Commissioners of Franklin County, Fla. Data analysis was supported by EPA Program Element #1 BA025 under Grant Number R-803339.

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DESCRIPTION OF ZOEAE OF COONSTRIPE SHRIMP, *PANDALUS HYPSINOTUS*, REARED IN THE LABORATORY

EVAN HAYNES[1]

ABSTRACT

Zoeae of *Pandalus hypsinotus* from ovigerous females caught in Kachemak Bay, Alaska, were reared in the laboratory. Each of the six zoeal stages is described and illustrated, and a brief description is given for postzoeal Stages VII-IX. The descriptions are compared with descriptions of zoeal stages of *P. hypsinotus* given by other authors.

Although pandalid shrimp form a major fishery resource along the Pacific coast of North America, little has been published on their early life history, especially on identification of the larval stages. Berkeley (1930) described the zoeal stages of five pandalid species from British Columbia, *Pandalus borealis* Krøyer, *P. danae* Stimpson, *P. hypsinotus* Brandt, *P. platyceros* Brandt, and *Pandalopsis dispar* Rathbun. The first zoeal stage of each species was obtained in the laboratory, and various remaining stages were obtained from the plankton. Berkeley also mentioned briefly the growth and distribution of the zoeae. Of 14 species of pandalid shrimps known to occur along the Pacific coast of North America, only two species, *Pandalus jordani* Rathbun and *P. platyceros*, have been reared through all their zoeal stages in the laboratory (Modin and Cox 1967; Price and Chew 1972).

In 1972, the National Marine Fisheries Service began an intensive investigation at its field station at Kasitsna Bay, Alaska, on the early life history of pandalid shrimp in Alaskan waters. The initial objective of the investigation was to describe in detail laboratory-reared zoeae of each pandalid species previously unverified. This report describes and illustrates each of the six zoeal stages of coonstripe shrimp, *P. hypsinotus*, and compares the stages obtained from laboratory-reared zoeae with stages obtained from the plankton by other authors. Brief descriptions of postzoeal Stages VII through IX are also included.

MATERIALS AND METHODS

Ovigerous *Pandalus hypsinotus* were caught at depths of 54 m (30 fathoms) in shrimp pots in late April 1973. They were kept in plastic buckets filled with seawater for about ½ h and then were put in plastic glass hatching boxes similar to those used by Price and Chew (1972) for rearing zoeae of spot shrimp, *P. platyceros*. The hatching boxes were kept in a biologically filtered recirculating aquarium system containing 190 liters (50 gallons) of refrigerated seawater, of which 19 liters (5 gallons) were exchanged for fresh seawater every other day. Salinity was maintained between 32 and 34‰ and temperature between 6° and 8°C. The quality and quantity of light were not controlled, but direct sunlight was avoided. Most zoeae were released at night but some were released during daytime whenever a female shrimp was stimulated to flex her abdomen rapidly. No predation of zoeae by female shrimp or by the zoeae themselves was noted. No prezoeae were seen.

About 50 zoeae were transferred by large-bore pipette to each of 25 500-ml beakers containing about 400 ml of aquarium seawater. In addition, a zoea was placed in each of 50 25- by 50-mm numbered plastic vials held in compartmented trays. The zoeae in the beakers provided both individual specimens and cast skins of various stages for dissection, and the individual zoeae in the vials provided a continuous sequence of cast skins with a known history. The beakers and vials were both checked daily for exuviae. Seawater in the holding containers was changed every other day and the zoeae were fed newly hatched nauplii of brine shrimp, *Artemia salina*, from San Francisco Bay.

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The density of nauplii was controlled only to the extent that a few nauplii remained in the container at the end of each feeding period. The original beakers and vials were used throughout the study because the zoeae also fed on the algae that grew on the sides and bottoms.

All zoeae molted at night. Of the deaths noted, most were caused by failure to complete the molting process; the posterior half was shed successfully, but the anterior half remained attached to the mouth parts and pereopods. Survival was about 90%.

Illustrations were drawn from unstained zoeae and from exuviae stained red with Turtox CMC-S[2] (acid fuchsin stain mountant). Stained exuviae show segmentation and setation more clearly than unstained. Zoeae and exuviae were dissected with the aid of a binocular dissecting microscope. The dissected material was mounted on a slide and drawn to scale with the aid of a camera lucida. Detail was checked with a compound microscope up to 430×.

In the final illustrations (Figures 1-6), for clarity, setules on the setae are usually omitted but spinulose setae are shown. Because the numbers of setae on the surface of the carapace and abdomen are highly variable, especially from Stage IV onward, they are figured only when useful in identification of a stage. For each pair of appendages the left member is figured except for the mandibles, which are drawn in pairs and figured from the right side. Whole zoeae are also figured from the right side. The figures are in part schematic and represent typical setal counts. The setation formulas proceed from the distal to the proximal ends of appendages. Gill development is mentioned in the text but usually not shown in the figures. The terms are defined as follows:

spinose—bearing many spines
spinous—spinelike
setose—set with bristles (setae)
spinulose—set with little spines.

Total length was measured from the anterior tip of the rostrum to the posterior tip of the telson with the aid of a dissecting microscope; the number of specimens used to determine total lengths is given for each stage. A minimum of 10 exuviae of each stage was used to verify segmentation and setation unless noted otherwise. The term "stage" denotes the intermolt period. Nomenclature of larval appendages and gills follows Pike and Williamson (1964) and Berkeley (1930) respectively.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

STAGE I ZOEA

Total length of Stage I zoea (Figure 1A) 5.8 mm (range 5.5-6.2 mm; 50 specimens). Live specimens brightly colored by numerous yellow chromatophores edged reddish brown. A conspicuous yellow chromatophore occurs dorsally on each eyestalk and at base of telson. Smaller but distinct chromatophores occur on nearly all appendages, especially maxillipeds and pereopods. Tips of antennule and antennal scale are tinged reddish brown. Chromatophore pattern of specimens preserved in 5% solution of Formalin and seawater for several days identical to the pattern on live specimens except that yellow color changes to reddish brown after preservation. Rostrum slender, spiniform, without teeth, about one-third length of carapace, and projects horizontally or slightly downward. Carapace with small, somewhat angular dorsal prominence at base of rostrum and a smaller rounded prominence near posterior edge; prominences occur in all zoeal stages. Antennal and pterygostomian spines present, but both usually hidden by sessile eyes; no supraorbital spine.

ANTENNULE (FIGURE 1B).—Antennule (first antenna) consists of a simple unsegmented tubular basal portion, distal conical base, distal conical projection, and a heavily plumose seta on a small conical base; distal conical projection bears four aesthetascs—one long, one short, and two of intermediate length.

ANTENNA (FIGURE 1C).—Antenna consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum two segmented and about one-fourth longer than scale; distal segment is styliform, tipped by a plumose seta and a spine. Distal segment may be partially segmented proximally. Protopodite bears spinous seta at base of flagellum and a spine at base of scale, both of which persist throughout zoeal development. Antennal scale distally divided into six segments (two proximal joints incomplete) and fringed with 10 heavily plumose setae along terminal and inner margins. A small seta occurs on outer margin near base of terminal segments.

MANDIBLES (FIGURE 1D).—Mandibles without palps. Incisor process of left mandible usually bears four teeth in contrast to the distinctly triserrate incisor process of right mandible. Left mandible bears one premolar denticle and right mandible bears two. Two subterminal processes occur on truncated molar process of left mandible but not on right mandible.

MAXILLULE (FIGURE 1E).—Maxillule (first maxilla) bears coxal and basial endites and an endopod. Proximal lobe (coxopodite) bears a stout seta near base and 12 spinulose setae terminally along with a series of extremely fine hairs. Median lobe (basipodite) bears 11 spinulose spines in two rows on terminal margin and several fine hairs subterminally. Endopodite originates from lateral margin of basipodite and bears three terminal and two subterminal setae; three of the five spines are sparsely plumose, the remaining two spinulose. There is no evidence of an outer seta (representing a vestigial exopodite) on maxillule.

MAXILLA (FIGURE 1F).—Maxilla bears platelike exopodite (scaphognathite) with 16 long, approximately equal, evenly spaced plumose setae along outer margin and one longer and slightly thicker seta (at proximal end). Endopodite has four partly fused segments and bears nine large plumose setae. Basipodite bilobed; each lobe bears eight setae. Bilobed coxopodite bears 16 setae, 4 on distal lobe and 12 on proximal lobe.

FIRST MAXILLIPED (FIGURE 1G).—First maxilliped most heavily setose of natatory appendages. Protopodite partially segmented; bears 7 setae on proximal segment and 18 slightly smaller setae on distal segment; most setae on protopodite plumose but some simple or spinulose. Endopodite distinctly four segmented; setation formula—4, 2, 1, 3. Exopodite a long slender ramus segmented at base; has four terminal and five or six lateral natatory setae. Epipodite a single lobe.

SECOND MAXILLIPED (FIGURE 1H). —Protopodite bisegmented; distal segment bears eight sparsely plumose setae, and proximal segment bears a simple seta. Endopodite distinctly five segmented; fourth segment expanded laterally; terminal segment has at least two spinulose setae; remaining setae on endopodite usually sparsely plumose; setation formula—7, 2, 1, 1, 3. Exopodite similar to exopodite of first maxilliped but slightly larger; has 4 terminal setae, 11 or 12 lateral natatory setae. No epipodite.

THIRD MAXILLIPED (FIGURE 1I).—Protopodite bisegmented; distal segment bears four setae. Endopodite distinctly five segmented and nearly as long as exopodite, giving it more pediform appearance than either of the two preceding appendages; setation formula —4, 8, 2, 2, 2. Exopodite similar to second maxilliped but slightly longer; has 3 or 4 terminal setae and 14 lateral natatory setae. No epipodite.

FIRST PEREOPOD (FIGURE 1J).—Endopodite functionally developed and similar in form to third maxilliped but slightly smaller. Endopodite distinctly five segmented; ends in simple conical dactylopodite; setation formula—3, 7, 2, 2, 2. Exopodite naked. Protopodite bisegmented; has four setae. Neither this nor remaining pereopods of this stage have any evidence of epipodite.

SECOND PEREOPOD (FIGURE 1K).—Second pereopod similar to first except that it has fewer setae and fourth or propodal joint is slightly extended to form beginning of chela.

THIRD, FOURTH, AND FIFTH PEREOPODS (FIGURE 1L-N).—These three pereopods essentially identical to each other except that they decrease slightly in size from third to fifth. No exopodites.

PLEOPODS.—No pleopods evident, not even as small buds.

TELSON (FIGURE 1O).—Telson not segmented from sixth abdominal segment; slightly emarginate distally; bears 14 densely plumose setae. Minute spinules at base of each seta; larger spinules along terminal margin between bases of four inner pairs and on the four inner pairs of setae themselves. Enclosed uropods visible. No anal spine.

STAGE II ZOEA

Total length of Stage II zoea (Figure 2A) 6.1

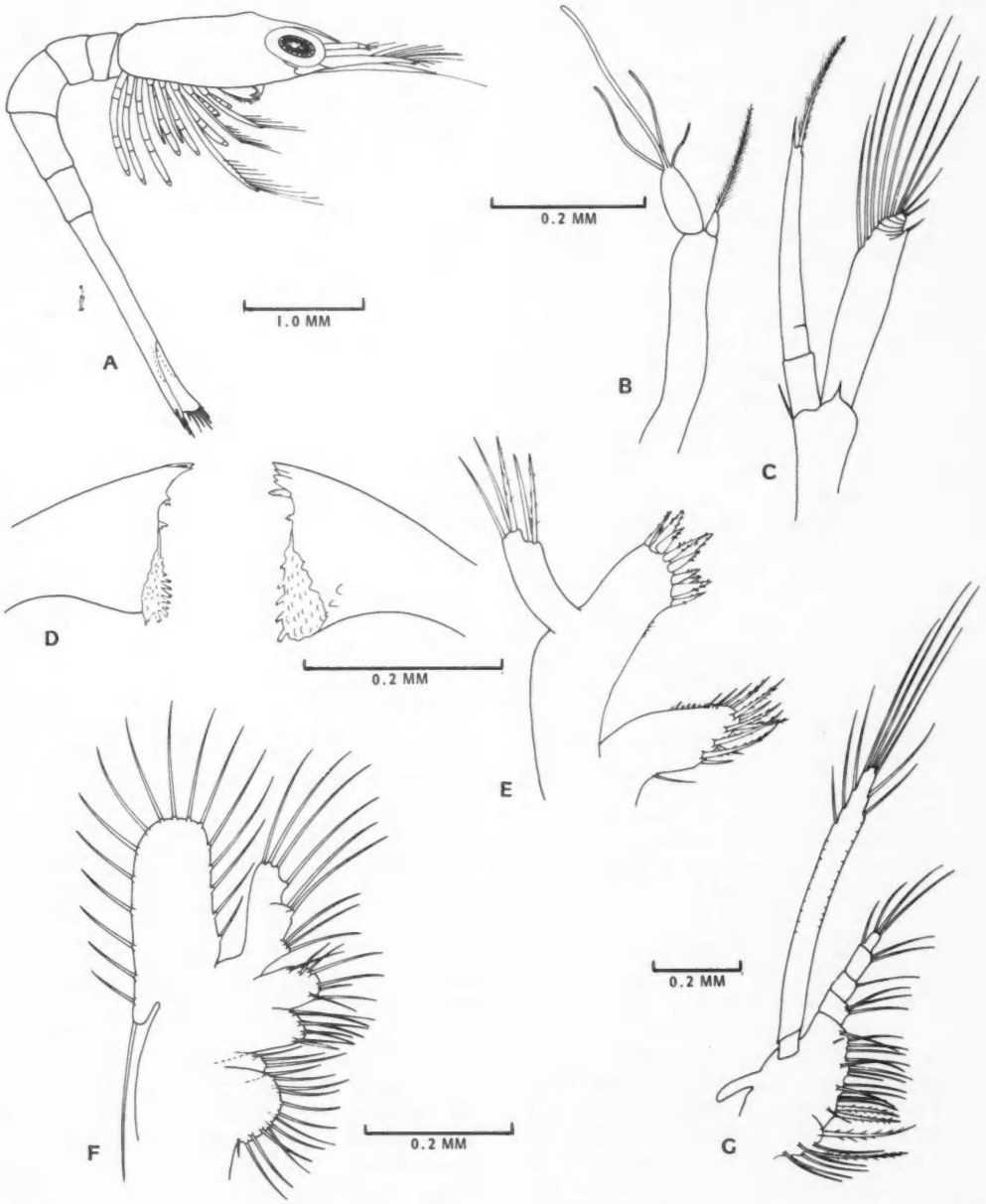
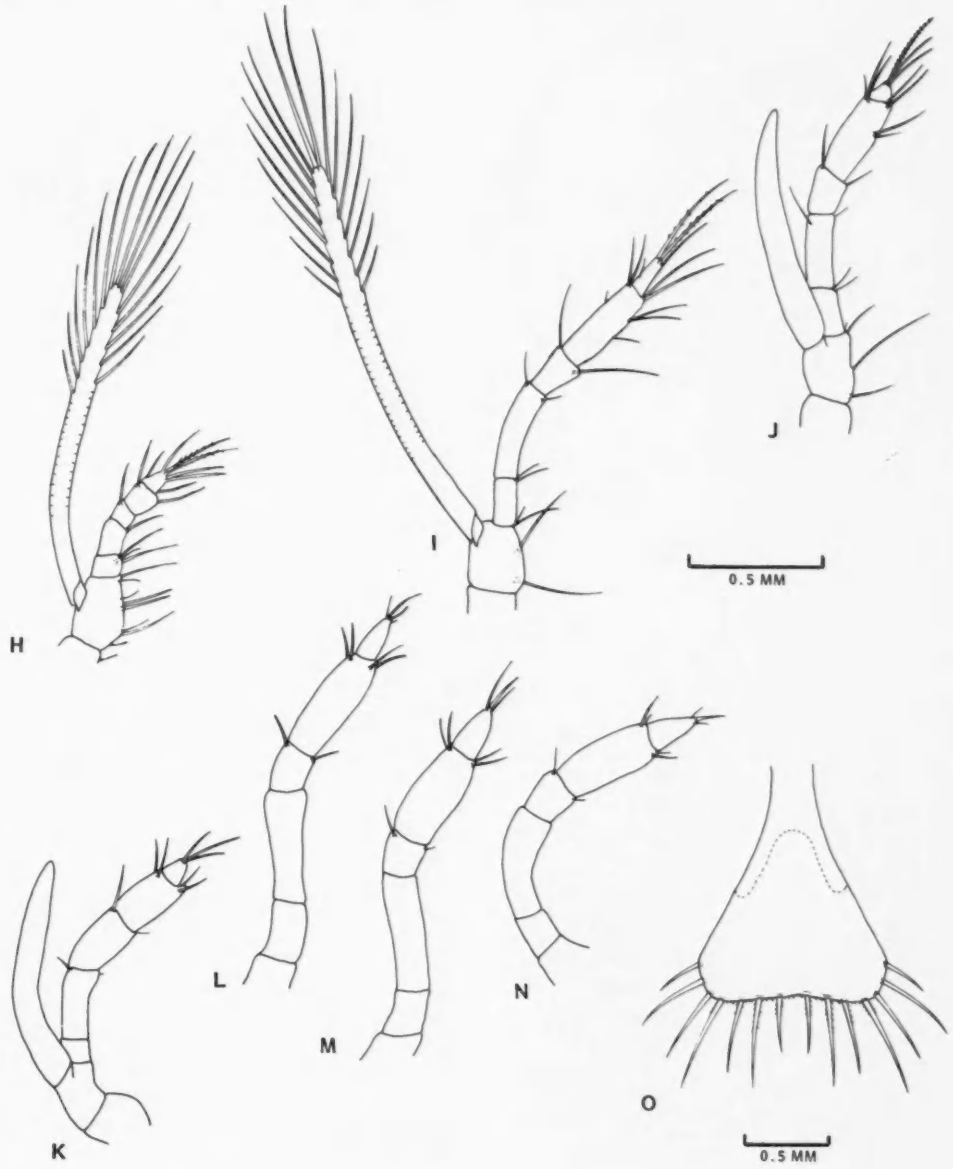


FIGURE 1.—Stage I zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandibles (right and left), (E) maxillule, (F) maxilla, (G) first maxilliped, (H) second maxilliped, (I) third maxilliped, (J) first pereopod, (K) second pereopod, (L) third pereopod, (M) fourth pereopod, (N) fifth pereopod, (O) telson.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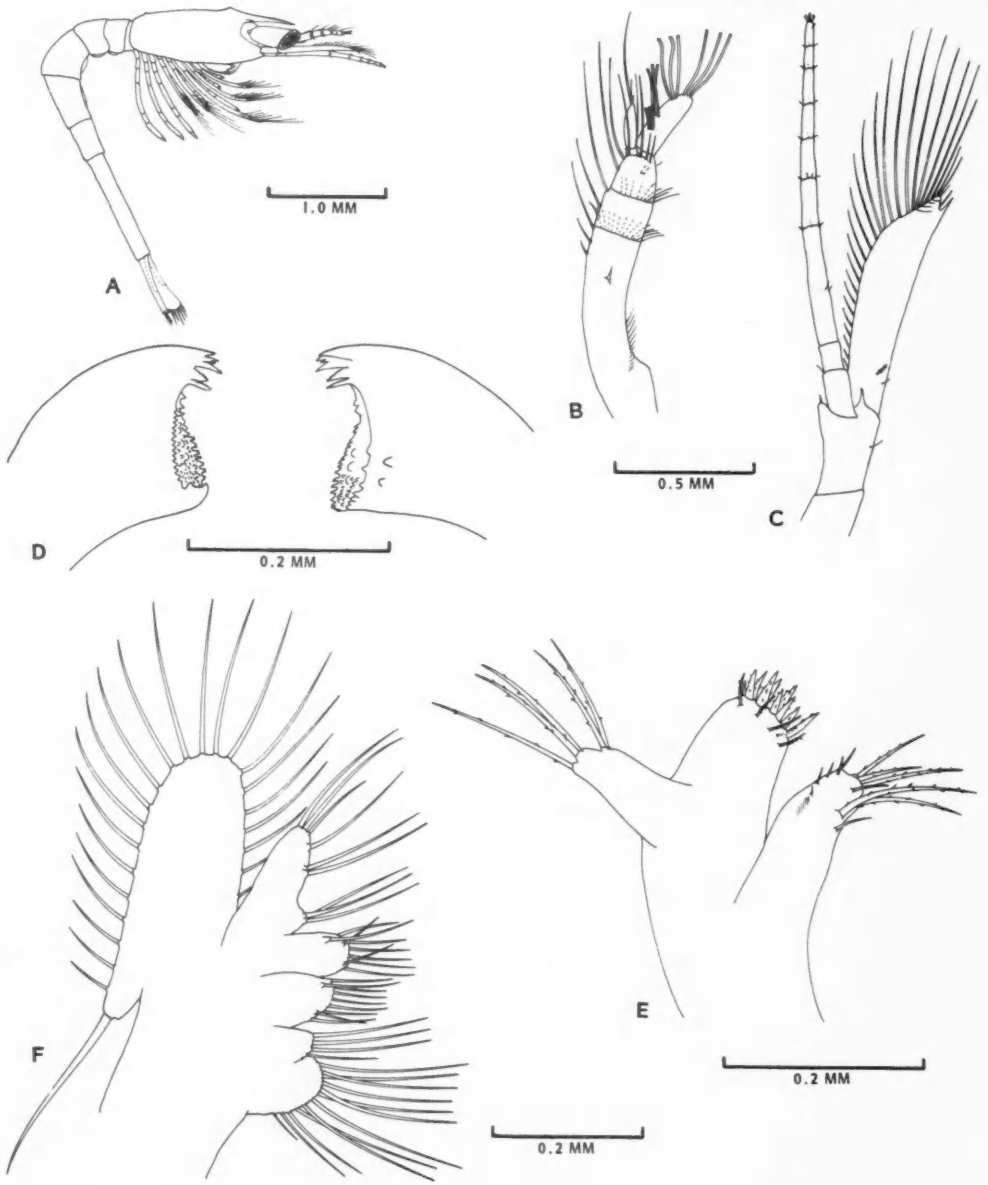
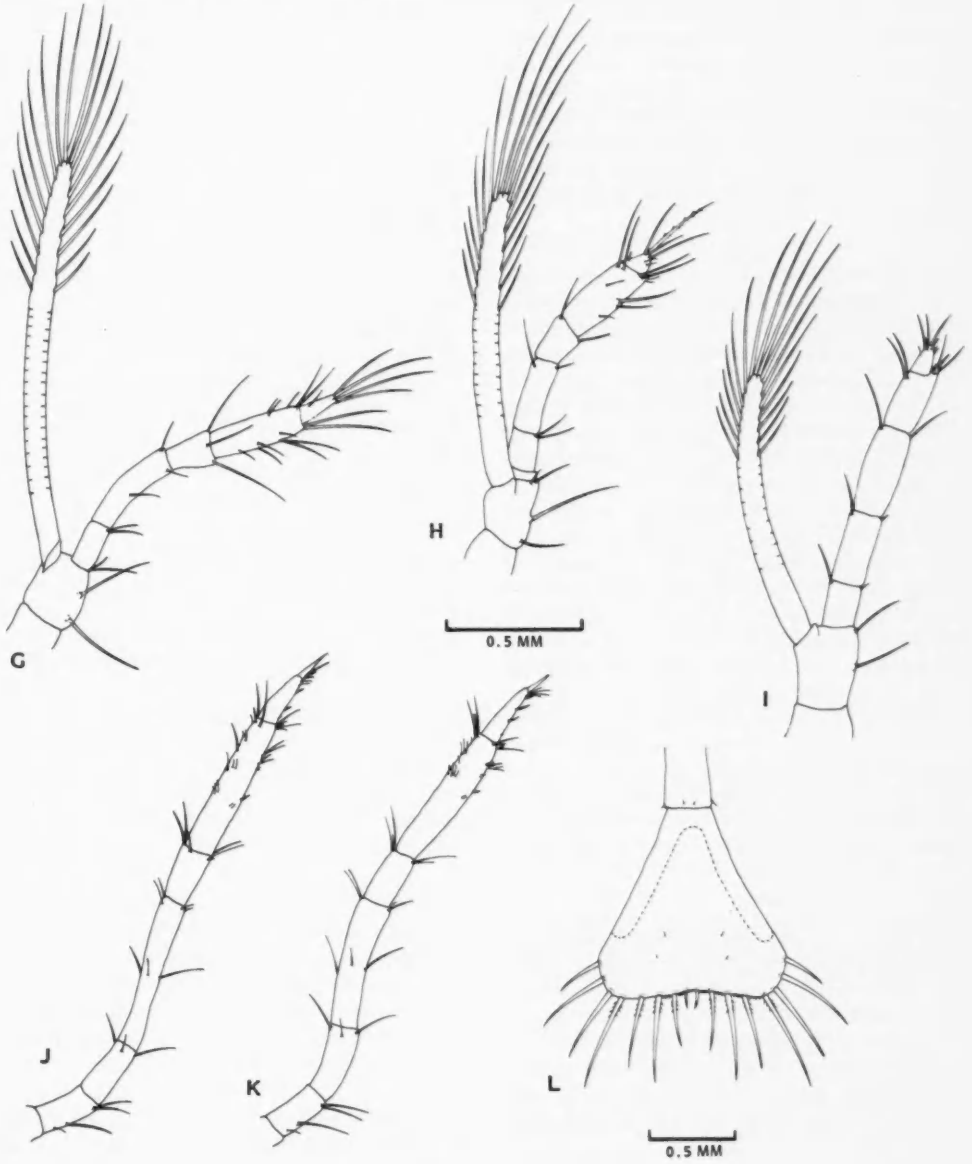


FIGURE 2.—Stage II zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandibles (right and left), (E) maxillule, (F) maxilla, (G) third maxilliped, (H) first pereopod, (I) second pereopod, (J) third pereopod, (K) fourth pereopod, (L) telson.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mm (range 5.6-6.5 mm; 50 specimens). Chromatophore color and pattern essentially identical to Stage I except ventral surface of abdomen now greenish. Rostrum still without teeth; not curved downward as strongly as in Stage I. Carapace same as Stage I except now has prominent supraorbital spine; antennal and pterygostomian spines clearly visible. Eyes, sessile in Stage I, now stalked.

ANTENNULE (FIGURE 2B).—Antennule shows considerable change from Stage I, now three segmented. It bears on terminal margin a large outer and a smaller inner flagellum, outer flagellum bears four groups of three aesthetascs each, one group terminally and three groups along inner margin; inner flagellum bisegmented and bears three setae terminally, one long and two short; originating at base of these two flagella is a dorsal budlike projection bearing four simple setae (projection and setae not shown in Figure 2B). Proximal segment of antennule laterally expanded at base, with about 12 small setae arranged laterally near expansion; 3 lateral plumose setae and about 14 dorsally projecting but smaller plumose setae ring terminal margin; large spine projects downward from ventral surface. Second segment has 4 lateral plumose setae, 2 long and 2 short, and about 10 dorsal plumose setae ringing terminal margin. Third segment has seven lateral plumose setae—five originating ventrally and the remaining two dorsally—and three simple setae—two dorsal and one lateral.

ANTENNA (FIGURE 2C).—Inner flagellum nine segmented, about twice as long as scale; distal segment tipped by about six small setae. Spine on basipodite at base of inner flagellum reduced in size. Antennal scale fringed with 28-30 long, thin plumose setae along terminal and inner margins. Joints at distal tip reduced to four, three of them incomplete. Distal outer seta of scale a stout spine.

MANDIBLES (FIGURE 2D).—More massive than in Stage I but still without palps. Both mandibles bear pair of premolar serrated denticles, and molar processes are more developed. Truncated end of molar process of right mandible formed into curved lip. Subterminal processes still present on left mandible.

MAXILLULE (FIGURE 2E).—Endopodite essentially unchanged from previous stage. Basipodite bears 10 spinose spines in two rows and five spinous setae on terminal margin, but no fine hairs. Coxopodite bears 12 setae terminally, 5 spinous and considerably longer than remaining 7.

MAXILLA (FIGURE 2F).—Similar to Stage I except exopodite larger and now bearing 21 or 22 marginal plumose setae in addition to plumose seta at proximal end. Lobes of basipodite bear nine setae each instead of eight as in Stage I.

FIRST, SECOND, AND THIRD (FIGURE 2G) MAXILLIPEDS.—Maxillipeds essentially identical to each other and nearly identical to first stage except for an increase in size and a slight variation in numbers of setae.

FIRST PEREOPOD (FIGURE 2H).—First pereopod functionally developed and similar in form to third maxilliped. Exopodites fringed with 15-17 plumose setae. Endopodite six segmented. Propodite projected slightly distally. Setae more numerous than in Stage I, especially on last two segments. This pereopod and the remaining four have a pleurobranchia bud at their base.

SECOND PEREOPOD (FIGURE 2I).—Similar to first pereopod except propodite projection longer and ischiopodite not segmented.

THIRD, FOURTH, AND FIFTH PEREOPODS (FIGURE 2J, K).—Third, fourth, and fifth pereopods essentially identical except for slight differences in size, fifth being smallest. Seven functional segments including dactylopodite. Dactylopodite bears spine at tip and three spines laterally. No exopodite.

PLEOPODS (FIGURE 2A).—Pleopods evident only as slightly swollen areas on abdominal segments.

TELSON (FIGURE 2L).—Telson distinct from sixth abdominal segment; bears 16 densely plumose setae along margin. Spinule arrangement essentially same as Stage I. Dorsal surface bears four small simple setae. Uropods still enclosed but longer than in first stage. No anal spine.

STAGE III ZOEA

Total length of Stage III zoea (Figure 3A) 6.7 mm (range 6.2-7.7 mm, 25 specimens).Chromatophore pattern similar to first two stages but less yellow color and more reddish brown. Rostrum pointing slightly upward with one or two small teeth at base. Supraorbital, antennal, and pterygostomian spines still present on carapace.

ANTENNULE (FIGURE 3B).—Outer flagellum distinctly three segmented; first and second segments have two groups of three aesthetascs each; distal segment has four aesthetascs. Inner flagellum still bisegmented but about twice as long as in Stage II. Remainder of antennule similar to Stage II except it is larger and more setose, and lateral projection on proximal segment is more arcuate.

ANTENNA (FIGURE 3C).—Antennal scale with 32-36 lateral plumose setae; no segmentation at tip in this or later stages. Lateral margin near base now has four additional simple setae. Flagellum about 3 times length of scale; has several additional segments and setae near base.

MANDIBLES (FIGURE 3D).—Both mandibles without palps. Right mandible bears three premolar processes; projections along anterior molar edge stronger and truncated end not curved into lip as in Stage II. Left mandible molar processes also stronger, and subterminal processes present.

MAXILLULE (FIGURE 3E).—Endopodite unchanged from Stage II except two setae particularly spinulose. Basipodite bears an additional plumose seta and a group of small fine hairs subterminally. Coxopodite now bears 14 instead of 12 setae and has more fine hairs than Stage II.

MAXILLA (FIGURE 3F).—Exopodite longer than in Stage II, slightly curved, and bears 27 marginal plumose setae in addition to plumose seta at proximal end. Lobes of basipodite bear 10 setae instead of 9 as in Stage II.

FIRST AND SECOND MAXILLIPEDS.—Epipodite on first maxilliped has rudiment of second lobe. Otherwise, first and second maxillipeds same as Stage II but slightly larger.

THIRD MAXILLIPED (FIGURE 3G).—Similar in shape to third maxilliped at Stage II but larger and more spinous and propodite bears two small spinulose spines. Numbers of setae on endopodites of maxillipeds and pereopods on this and succeeding stages are so highly variable that a specific description of them would not be an aid in identification of stage or species.

FIRST PEREOPOD (FIGURE 3H).—Exopodite still present, more setose than Stage II. Propodite bears a small spinulose spine near base. Pleurobranchia at base of this appendage and remaining four pereopods barely larger than in Stage II.

SECOND PEREOPOD (FIGURE 3I).—Most significant changes are presence of chela on endopodite and an additional segment on base of ischiopodite.

THIRD (FIGURE 3J), FOURTH, AND FIFTH PEREOPODS.—Essentially similar; fifth smallest as usual. Greater development from Stage II shown by well-formed dactylopodite and more setae. An additional segment occurs at base of ischiopodite.

PLEOPODS (FIGURE 3A).—Pleopods evident as small buds.

TELSON (FIGURE 3K).—Uropods free; bear plumose setae and small, randomly located setae on dorsal surface. Telson broader at tip than at base and still slightly emarginate; bears seven pairs of spinous setae and two pairs of lateral spines. Base of telson bears a pair of simple setae that increase in number in later stages and persist in adults. Anal spine appears at this stage.

STAGE IV ZOEA

Total length of Stage IV zoea (Figure 4A) 7.5 mm (range 7.3-8.1 mm, 10 specimens). Chromatophore pattern and color considerably different from previous stages. In general, numerous small wine-red chromatophores occur on carapace, pereopods, and ventral surface of abdomen; small yellow chromatophores occur on carapace, antennules, antennal scale, uropods, telson, and third abdominal segment. Rostrum beginning to acquire adult shape; 11-13 dorsal spines, 2 or 3 small ventral spines, and 1 dorsal spine that may be

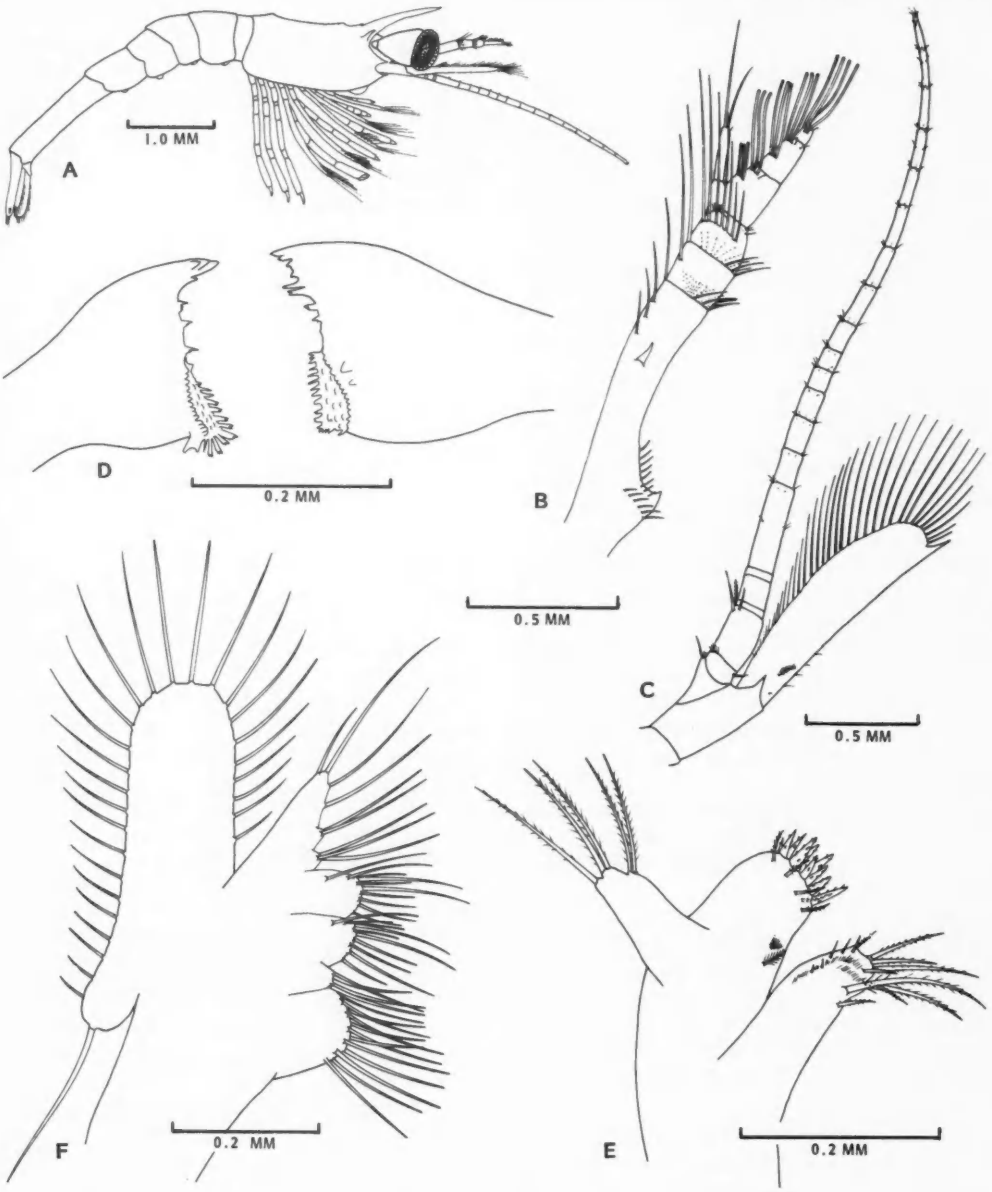
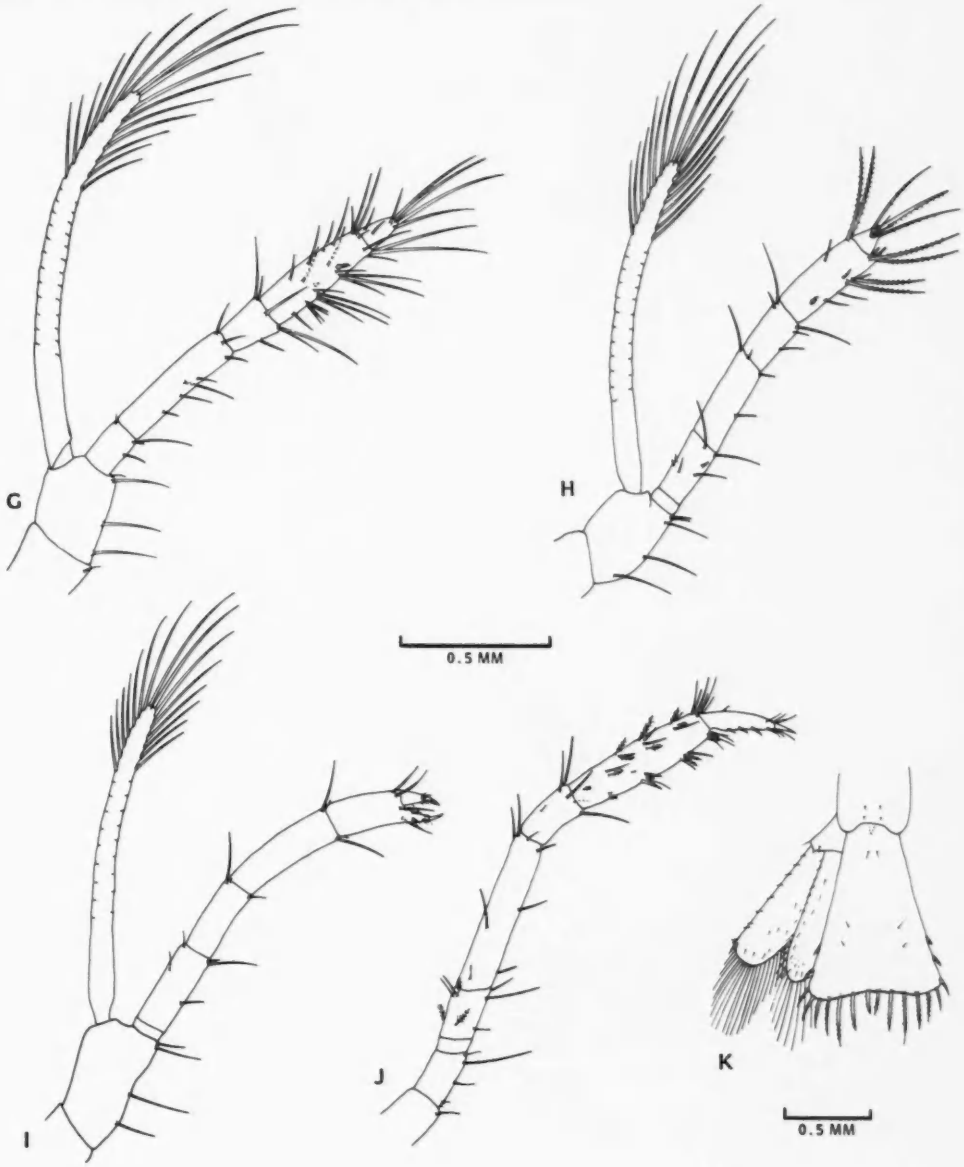


FIGURE 3.—Stage III zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandibles (right and left), (E) maxillule, (F) maxilla, (G) third maxilliped, (H) first pereopod, (I) second pereopod, (J) third pereopod, (K) telson.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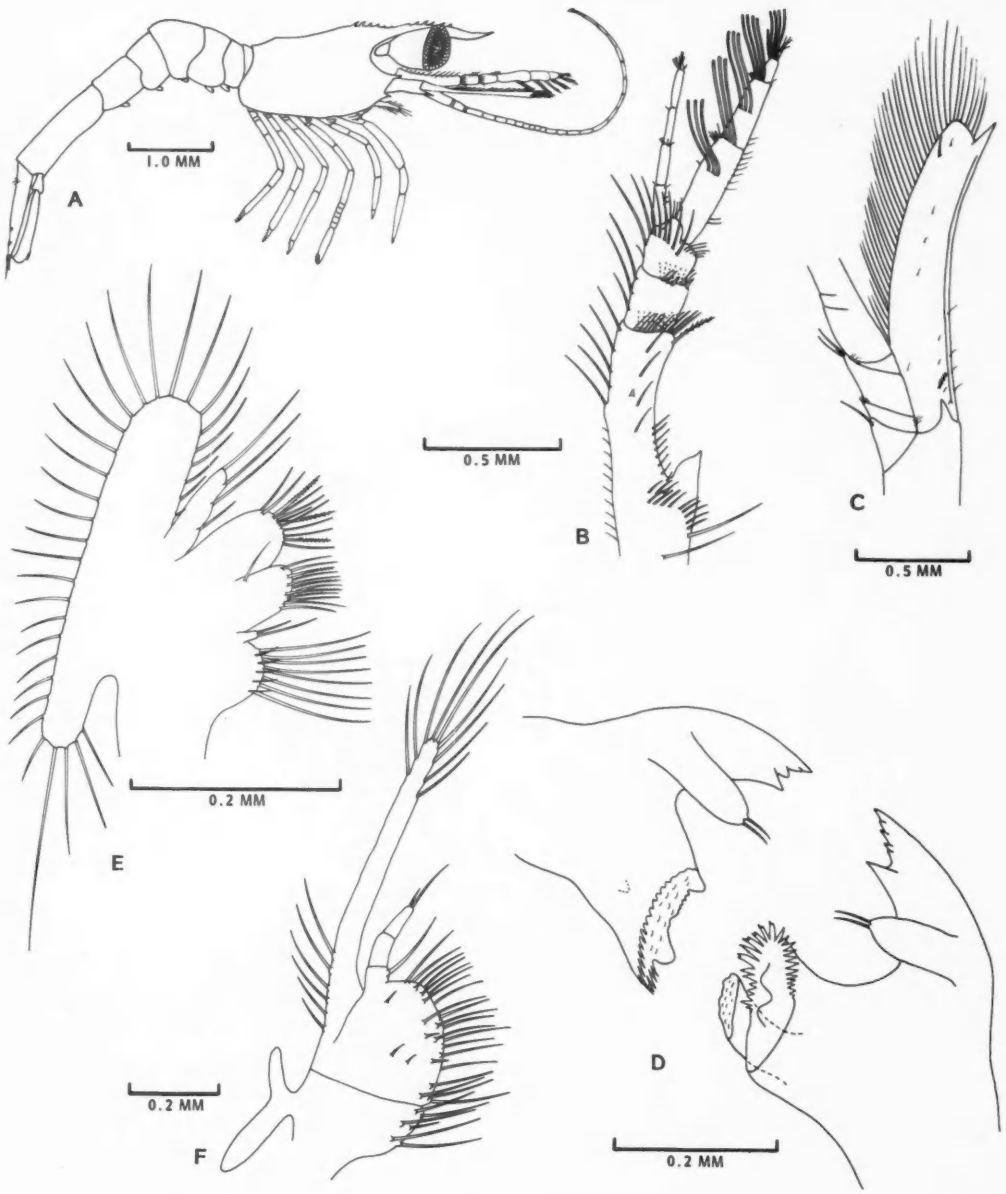
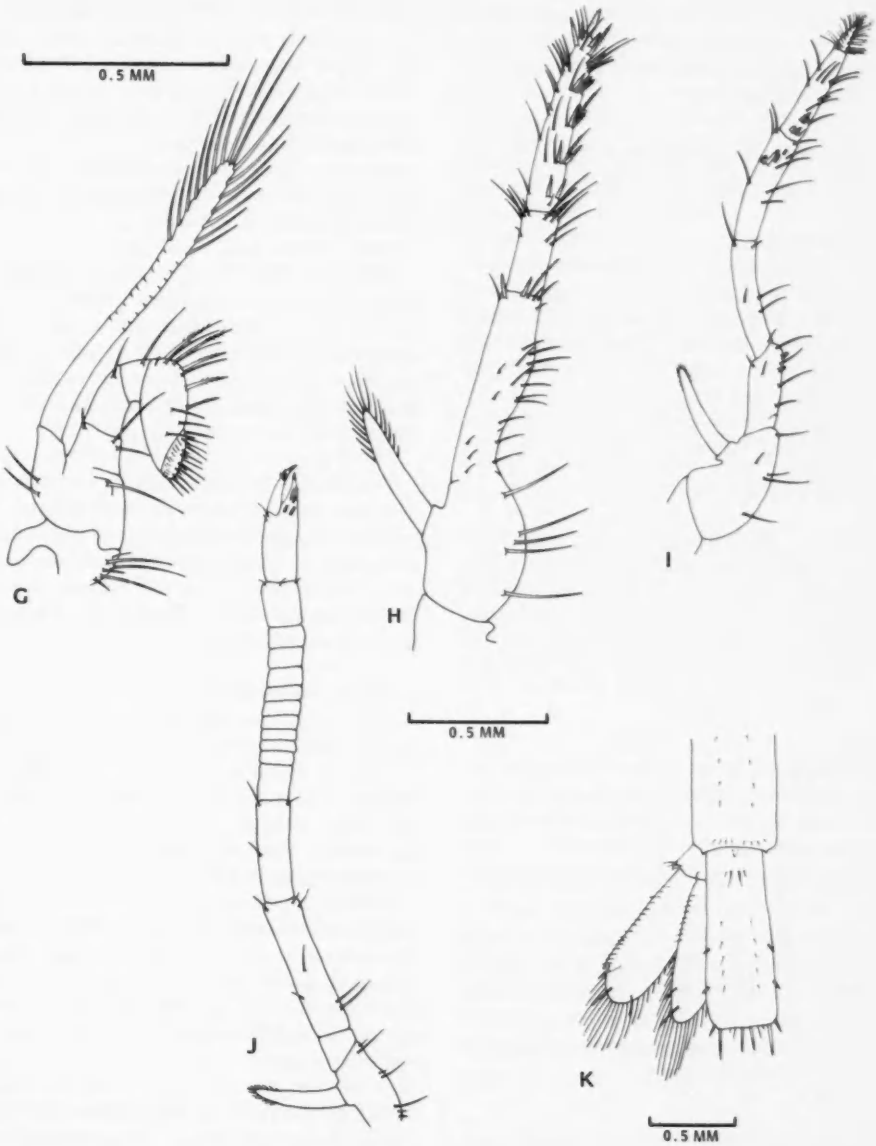


FIGURE 4.—Stage IV zoea of *Pandalus hypsinotus:* (A) whole animal, (B) antennule, (C) antenna, (D) mandible (right and left), (E) maxilla, (F) first maxilliped, (G) second maxilliped, (H) third maxilliped, (I) first pereopod, (J) second pereopod, (K) telson.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faint or distinct near acute tip. No supraorbital spine in this or remaining stages (Figure 4A). Small setae and groups of minute hairs irregularly located on carapace.

ANTENNULE (FIGURE 4B).—Outer flagellum four segmented and longer than in Stage III beginning to acquire slender terminal portion as in adult; five groups of aesthetascs, two groups on first and second segments each and one group on third; groups composed of 3, 3, 3, 4, and 5 aesthetascs. Inner flagellum four segmented, nearly as long as outer flagellum. Rest of antennule similar in shape to Stage III but larger; bears additional spines and setae; lateral projection on proximal segment more pronounced, and ventral spine on proximal segment noticeably smaller than in Stage III.

ANTENNA (FIGURE 4C).—Antennal scale with 32-39 lateral plumose setae and is assuming narrow, slightly curved form of adult; scale bears a few simple setae medially and usually a large seta on inner margin near tip. Inner flagellum not much longer than Stage III, about 3½ times length of scale.

MANDIBLES (FIGURE 4D).—Incisor and molar processes of both mandibles separated by deep cleft, and each mandible has unsegmented palp bearing two setae terminally. Curved lip of right mandible considerably larger than in Stage III.

MAXILLULE.—Similar to Stage III except number of setae somewhat variable. Endopodite usually has one seta but may bear additional small setae. Basipodite has 12 spines and 9-13 setae terminally, 2 or 3 setae subterminally. Coxopodite usually has 15 setae.

MAXILLA (FIGURE 4E).—Exopodite fringed, has 32 plumose setae in addition to plumose seta at proximal end; separated from protopodite by cleft and bears 3 setae along inner margin. Number of setae on endopodite reduced to four. Basipodite bears 12 setae on each lobe; proximal lobe bears additional seta subterminally. Distal lobe of coxopodite reduced in size and bears two setae instead of four as in Stage III; proximal lobe of coxopodite bears eight long and five short setae.

FIRST MAXILLIPED (FIGURE 4F).—Epipodite distinctly bilobed. Protopodite clearly two segmented and bears 6 setae on proximal segment, 26 smaller setae on distal segment. Endopodite three segmented and bears one long seta on first segment and one long and one short setae terminally on third segment. Exopodite bears 6 long plumose setae along proximal outer margin and 9 or 10 natatory setae.

SECOND MAXILLIPED (FIGURE 4G).—Second maxilliped has undergone considerable change from Stage III and now is similar in shape to adult. Endopodite five segmented; terminal segment flattened with many short spinous setae on lateral margins. Epipodite arises from coxopodite and is single lobed.

THIRD MAXILLIPED (FIGURE 4H).—Exopodite considerably reduced. Endopodite heavily setose and spinous. Meropodite slightly enlarged medially; not distinctly segmented from ischiopodite. Basipodite enlarged medially somewhat more than meropodite. Bud of mastigobranchia arises from coxopodite.

FIRST PEREOPOD (FIGURE 4I).—Exopodite reduced as in preceding appendage. Endopodite ends in simple, heavily setose conical dactyl, as in the third maxilliped; ischiopodite articulates somewhat laterally with meropodite. Pereopods of this stage, except fifth pair, bear bud of mastigobranchia. Each pleurobranchia adult in shape and clearly lobulated.

SECOND PEREOPOD (FIGURE 4J).—Exopodite reduced in size as in third maxilliped and first pereopod. Joints appear on carpal segment for first time, 10 or 11 on left and 5-7 on right. Left pereopod slightly longer (about one-tenth) than right pereopod.

THIRD, FOURTH, AND FIFTH PEREOPODS.—Essentially similar to pereopods of Stage III.

PLEOPODS (FIGURE 4A).—Pleopods cleft slightly and without joints or setae.

TELSON (FIGURE 4K).—Lateral margins nearly parallel but spaced slightly wider posteriorly and bear two spines on each margin. Terminal margin straight and bears three pairs of feathered spines, the second pair longest; two

simple setae—one long, one short—occur between first and second pairs of spines. Two pairs of simple setae (inner pair stouter) occur at base of telson and project noticeably at nearly right angles to telson surface (Figure 4A). Both pairs of uropods nearly as long as telson and fully developed; both bear numerous small setae irregularly located on dorsal and ventral surfaces of both pairs in addition to setae figured. Beginning of transverse hinge (diaeresis) of exopodite of uropod faintly evident.

STAGE V ZOEA

Total length of Stage V zoea (Figure 5A) 9.2 mm (range 8.4-10.1 mm, 10 specimens). Numerous small wine-red chromatophores occur primarily on cephalothorax but also along surface of abdomen to base of telson and on dorsal hump of third abdominal segment; large wine-red chromatophore on side of carapace especially pronounced; yellow chromatophores few and minute; occur in head region at base of antennae, on antennules, and on dorsal surface of eyes. Rostrum similar in shape to adult; 15-17 dorsal teeth, in addition to 1 (rarely 2) near acute tip; 4 or 5 ventral teeth. Still no setae between dorsal rostral teeth (Figure 5A).

ANTENNULE AND ANTENNA.—Essentially similar to Stage IV. Inner flagellum of antenna approximately 4 times length of scale.

MANDIBLES.—Mandibles larger but morphology unchanged from Stage IV; mandibular palp row three segmented and bears three or four setae terminally (Figure 5B).

MAXILLULE (FIGURE 5C).—Maxillule adult in shape. Endopodite bears one long seta terminally, sometimes an additional short seta. Basipodite bears 13 spines in two rows along terminal margins: 5 of the spines are relatively long and the remaining 8 short. Seventeen setae of various lengths are distributed terminally and along lateral margin of basipodite. Coxopodite bears five long spinulose setae terminally and a row of five shorter sparsely plumose setae extending proximally; row of fine hairs and a medial seta occur ventrally.

MAXILLA (FIGURE 5D).—Maxilla more adult in shape than previously. Exopodite fringed with 40-44 plumose setae; proximal expansion of exopodite and setae along its inner margin, especially proximal seta, considerably longer than in previous stages. Endopodite shaped as adult; bears three setae. Shape and setation of basipodite and coxopodite similar to Stage IV except distal lobe of basipodite bears 15 setae and proximal lobe of coxopodite bears 7 long and 5 short setae.

FIRST AND SECOND MAXILLIPED.—Similar to Stage IV except endopodite of first maxilliped bears two setae on second segment and three or four on proximal segment.

THIRD MAXILLIPED.—Similar to Stage IV except for a few additional setae, and exopodite is reduced to remnant. Mastigobranchia similar in shape to adult. Arthrobranchia small bud.

FIRST PEREOPOD.—Appendage with few additional setae and spines. Exopodite remnant, distal joint of ischiopodite more pronounced than in Stage IV (Figure 5E). Arthrobranchia minute bud. Mastigobranchia on this and pereopods two to four; adult in shape.

SECOND PEREOPOD.—Exopodite remnant, carpal joints of left and right pereopods 14-16 and 7. No arthrobranchia on this or remaining pereopods.

THIRD, FOURTH, AND FIFTH PEREOPODS.—Distal joints of carpal and basial segments pointed (Figure 5F), no additional joint at basis. Setation essentially as shown in Figure 3J except carpopodite and meropodite each bear a spine.

PLEOPODS (FIGURE 5A).—Pleopods bilobed, segmented, and without setae.

TELSON (FIGURE 5G).—Lateral margins nearly parallel but slightly farther apart at center and bear two spines on each margin. Terminal margin straight; arrangement of spines and setae on margin similar to Stage IV. The two pairs of setae at base of telson noticeably longer than in Stage IV. Transverse hinge of exopodite of uropod complete; numerous small setae located randomly on dorsal and ventral surfaces in addition to those figured.

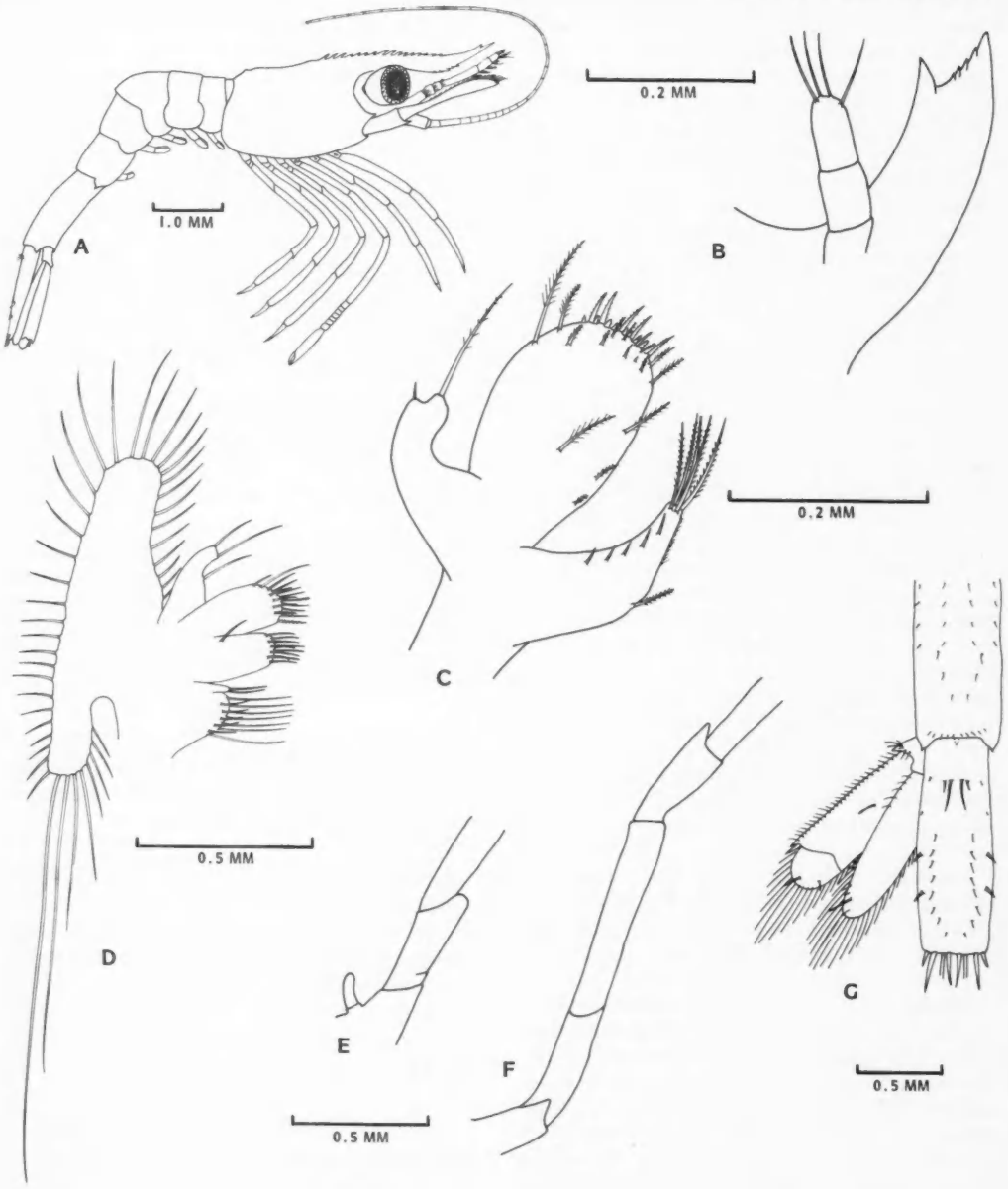

FIGURE 5.—Stage V zoea of *Pandalus hypsinotus:* (A) whole animal, (B) mandibular palp, (C) maxillule, (D) maxilla, (E) first pereopod, (F) fifth pereopod (segmentation only), (G) telson.

STAGE VI ZOEA

Total length of Stage VI zoea (Figure 6A) 10.8 mm (range 10.0-11.8 mm, 10 specimens). General color wine-red, particularly on carapace and pereopods and along ventral abdomen; remainder of telson greenish hue. Most appendages of this stage differ in shape only slightly from those of Stage V and succeeding stages and are not figured in detail. Rostrum with 15-19 dorsal teeth in addition to 1 (usually) but sometimes 2 dorsal teeth near acute tip; 4-7, usually 5, ventral teeth. A seta may occur between two or three dorsal teeth (Figure 6A).

ANTENNULE.—Inner flagellum six segmented (rarely five). Outer flagellum eight segmented; bears seven (rarely eight) groups of three (usually) aesthetascs each.

ANTENNA.—Antennal scale fringed with 40-45 plumose setae; flagellum about 6 times length of scale.

MANDIBULAR PALP.—Three segmented; number of setae variable; setation formula—6-8, 2-3, and 1-3.

MAXILLULE.—Endopodite unchanged from Stage V. Basipodite bears about 20 setae and 13 spines; coxopodite bears 18 setae.

MAXILLA.—Exopodite fringed with 61 or 62 plumose setae. Three setae on endopodite. Setation formula of lobes of basipodite and coxopodite 21-22, 17-19, 2, 11-12.

FIRST MAXILLIPED.—Exopodite has 10 or 11 setae along proximal margin. Setation formula of endopodite 2, 4, 5. Number of setae on protopodite variable—38-61 on basipodite, 7-12 on coxopodite.

SECOND MAXILLIPED.—More setose than in preceding stages; about 50 setae on terminal segment. No podobranchia.

THIRD MAXILLIPED.—No exopodite. Arthrobranchia as two minute rounded buds.

FIRST PEREOPOD.—No exopodite. Arthrobranchia bud at base of each pereopod except fifth.

SECOND PEREOPOD.—No exopodite; carpal joints of left and right pereopods 19 and 7 or 8 respectively. Left and right meropodites with three or four and one or two joints respectively.

THIRD, FOURTH, AND FIFTH PEREOPODS.—Meropodite bears 4-6 spines. Fifth pereopod bears neither bud of arthrobranchia nor epipodite.

PLEOPODS (FIGURE 6B).—All five pairs segmented, biramus, and tipped with setae but nonfunctional. Appendix interna small bud on inner lamella of second and third pleopods only.

TELSON (FIGURE 6C).—Telson shows, for first time, narrow shape similar to adult and bears three pairs of dorsolateral spines. Terminal margin rounded slightly; bears three pairs of feathered spines and a pair of large setae dorsally. Three pairs of stiff setae at base of telson instead of two as in Stage V.

POSTZOEAL STAGES VII-IX

Total length of Stage VII zoea 12.1 mm (range 11.5-12.8 mm, four specimens). Pleopods functional and appendix interna distinct on all pleopods except first pair. Because abdominal propulsion is evident at this stage, it is considered the first postzoeal (megalopa) stage (Williamson 1969). Dorsal rostral spines 19 or 20, 1 or 2 at acute tip; 7 or 8 ventral spines. Seta (usually 1, rarely 2) occurs between each pair of rostral spines. Bud of podobranchia distinct, arises at base of epipodite of second maxilliped; buds of arthrobranchiae on third maxilliped distinct, pointed. Telson bears four pairs of spines along lateral margin, rarely an additional small spine on either margin. Left and right carpal joints of second pereopods 24 or 25 and 10 respectively.

Stages VIII and IX differ only slightly from VII. Total length of Stage VIII zoea 12.4 mm (range 11.1-13.0 mm, four specimens). Gill buds more fully developed in VIII than in VII but not yet lobulated. Left and right carpal joints of second pereopod 28 and 10 or 11 respectively. Total length of Stage IX zoea 13.6 mm (range 13.4-13.8 mm, three specimens). Rostrum with one to three setae between dorsal rostral spines and one to five setae between ventral spines; seta between the two spines at rostral tip. Buds of both podobranchiae and arthrobranchiae nearly lobulated.

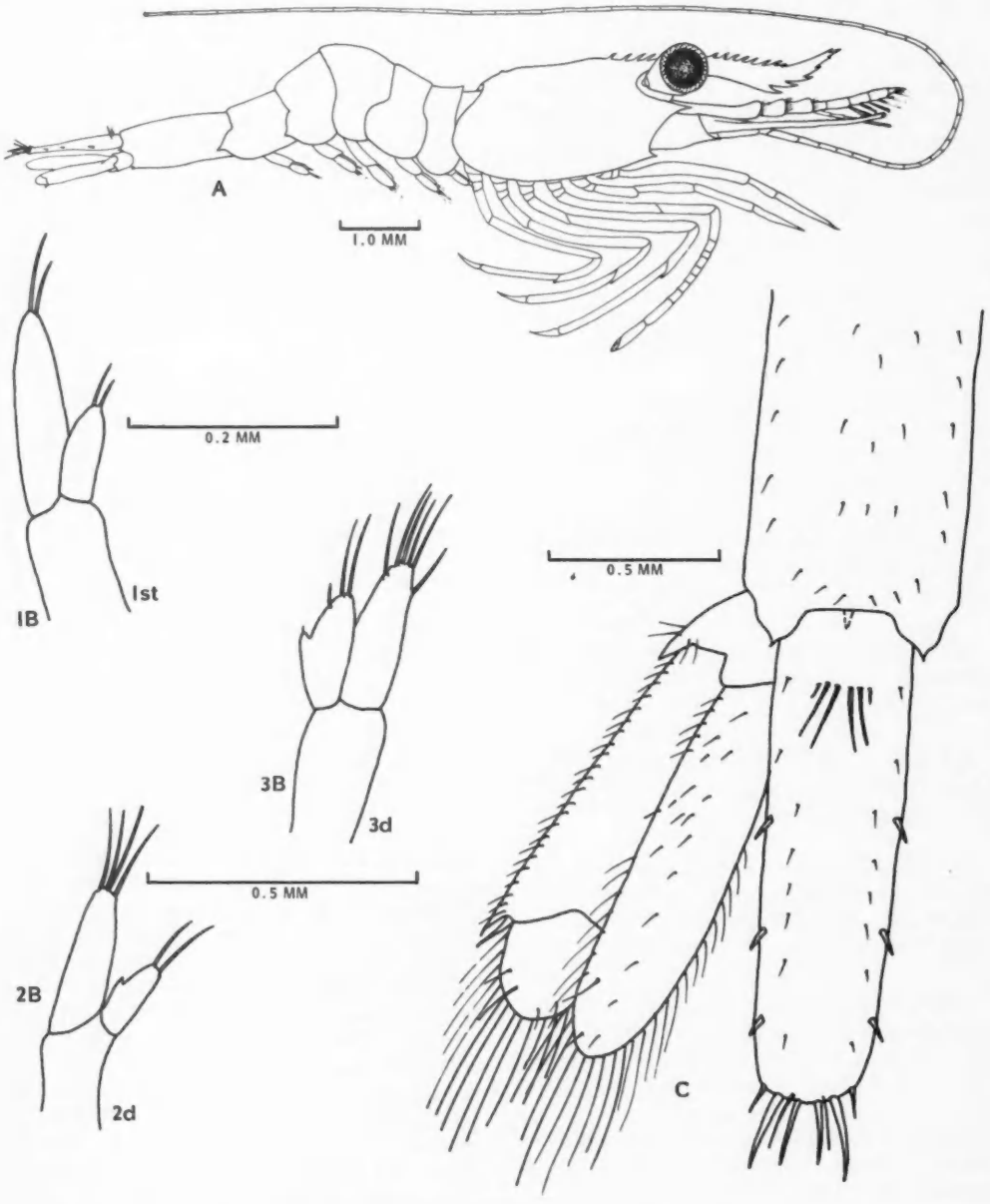

FIGURE 6.—Stage VI zoea of *Pandalus hypsinotus:* (A) whole animal, (B) pleopods (1, 2, and 3), (C) telson.

COMPARISON OF ZOEAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

Berkeley (1930) described and figured the first stage zoeae of *P. hypsinotus* that she reared in the laboratory. She also obtained the probable second and third stages from the plankton, but these were not described. Stage I zoeae reared by Berkeley differed in several respects from mine, but mostly in segmentation and setation of appendages. For instance, Berkeley showed the telson separated from the sixth abdominal segment by a joint whereas I do not. She described the tip of the antennal scale as unsegmented, but my zoeae have the tip divided into six segments. The endopodites of the first and second maxillipeds of her zoeae are unsegmented, and the exopodites of the maxillipeds and first and second pereopods are unjointed at their bases. In my zoeae, the endopodites of the first and second maxillipeds are segmented, and the exopodites of the maxillipeds and first and second pereopods are jointed at their bases. Segmentation of appendages, especially in the early zoeal stages, is most clearly seen in exuviae. Because Berekeley was unable to obtain exuviae from her laboratory-reared specimens, she probably missed seeing the segmentation of most appendages.

Kurata's (1964) description of Stage I zoeae of *P. hypsinotus* was also based on specimens reared in the laboratory; the remaining stages (II-V) he described were obtained from the plankton. The most important differences between Kurata's description and mine are: Stage I—Kurata's zoeae bear a chela on the second pereopod and the antennal scale is four segmented. In my zoeae the chela does not appear until Stage III and the antennal scale is six segmented. Stage II—The tip of the antennal scale is two segmented in Kurata's zoeae but four segmented in mine. Stage III—On Kurata's zoeae, the marginal spines of the telson vary from one to three pairs, and the inner flagellum of the antenna is twice as long as the antennal scale and has 9 or 10 joints. My Stage III zoeae always have two pairs of marginal spines and the inner flagellum of antenna is 3 times the length of the antennal scale and has 19 joints. Stage IV—The telson of Kurata's zoeae decreases in width posteriorly; the inner flagellum of antennule is two segmented; the tip of the first pereopod bears a small chela; and the carapace bears a supraorbital spine. The telson of my Stage IV zoeae increases in width posteriorly; the inner flagellum of antennule is four segmented; the tip of the first pereopod bears a simple dactylopodite in all stages (including adults); and the supraorbital spine occurs only in Stages II and III. Stage V—The telson of Kurata's zoeae bears 6+6 spines terminally; the carpopodites of the second pereopods and the pleopods are without joints; and the carapace still bears a supraorbital spine. In my specimens, the telson bears 3+3 spines terminally; the carpopodites of the left and right second pereopods bear 14-16 and 7 joints respectively; the pleopods are jointed; and the carapace does not bear a supraorbital spine.

The cause for the morphological differences between Kurata's description of the morphology of the zoeae and mine is unknown but apparently is not a result of my zoeae being reared in the laboratory. My zoeae showed no variation in number of zoeal stages and only negligible morphological variation between individuals of the same stage. Also, there were no morphological differences between my zoeae reared in the laboratory and the zoeae of *P. hypsinotus* available from local plankton collections (Stages I-III). The morphological differences between Kurata's zoeae and mine may be due to geographical variation. Berkeley (1930) has shown that pandalid zoeae from the northeast Pacific are further advanced on hatching than those from the Atlantic, although she did not have enough information to compare identical species from both areas. Unfortunately, Kurata's descriptions from Stage II onward were based on specimens from the plankton. Verification of geographical variation in zoeal morphology will be possible only when identification is based upon zoeae of known parentage and the magnitude of variation is established for each stage.

Segmentation of the antennal scale was used by Lebour (1940) as one criterion for classifying the early stages of pandalid zoeae into two groups. The first group includes pandalid species described by various authors as possessing a segmented scale (*Dichelopandalus bonnieri* (Caullery), *Pandalus montagui* Leach, and *P. propinquus* G. O. Sars). The second group includes pandalid species described by Berkeley (1930) as possessing an unsegmented scale (*P. stenolepis* Rathbun, *P. hypsinotus, P. danae*, and *P. platyceros*). Price and Chew (1972) showed Lebour's grouping to be invalid for *P. platyceros*. Kurata (1964) described zoeae of *P. hypsinotus* as hav-

ing a segmented scale. Laboratory-reared Stage I zoeae known by me to possess a segmented scale are *Pandalopsis dispar, Pandalus stenolepis, P. goniurus, P. borealis, P. danae, P. hypsinotus,* and *P. platyceros.* Berkeley obviously failed to recognize the segmented scales on her specimens. Therefore, Price and Chew's (1972) suggestion that Lebour's grouping for classifying the early stages of pandalid zoeae using segmentation of the antennal scale be disregarded is valid.

In most Decapoda, the development of functional pleopods provides a convenient and clear distinction between the zoeal and postzoeal stages because it is accompanied by several other abrupt changes in morphology, such as loss or reduction of some or all of the thoracic exopodites and changes in shape and body proportions. In the Pandalidae, however, there is not always an abrupt metamorphosis at this molt. Pike and Williamson (1964) discussed how in *P. montagui* the pleopods may become fully functional before the exopodites on the pereopods show any reduction; in *P. danae* the exopodites on the pereopods and the third maxilliped degenerate before the pleopods become functional; and in *P. kessleri* Czernaivski the exopodites on the pereopods never become functional. In my zoeae the development of functional pleopods occurred at Stage VII, but other morphological changes normally associated with postzoeal metamorphosis occurred earlier, especially at the molt to Stage IV. Morphological changes that occurred at the molt to Stage VI are reduction of thoracic exopodites; loss of supraorbital spines; changes in color; changes in shape of rostrum, mandibles, and second maxilliped; and segmentation of carpopodite of the second pereopod. Depending upon one's definition of "megalopa," it may be valid to consider Stage VII of *P. hypsinotus* as the megalopa; or one may consider stages IV through VII are all megalopal or the term "megalopa" is not strictly applicable to *P. hypsinotus.*

In addition to the morphological changes noted above, abbreviated development of zoeae of *P. hypsinotus* is also indicated by the occurrence of thoracic exopodites on pereopods 1 and 2. In contrast, most Pandalidae without abbreviated development have thoracic exopodites on pereopods 1-3. A notable exception is zoeae of *P. platyceros,* which have thoracic exopodites on pereopods 1-3 but only four zoeal stages and 8+8 telson setae in Stage I rather than the usual 7+7. Another feature of abbreviated development in *P. hypsinotus* is the proximal extension and occurrence of 17 setae on the exopodite of the maxilla in Stage I. Usually the exopodite of the maxilla in Stage I of the Caridea has no proximal extension and only five setae, as in the protozoea of the Peneidea and most British Pandalidae (Lebour 1940; Gurney 1942). The abbreviated development of zoeae of *P. hypsinotus* agrees with the findings of Berkeley (1930), who noted that zoeae of most Pandalidae of the northeast Pacific tend to be more developed when they hatch than is normal for Caridea.

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PRESENT AND HISTORICAL SPAWNING GROUNDS AND NURSERIES OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*, IN THE DELAWARE RIVER[1]

MARK E. CHITTENDEN, JR.[2]

ABSTRACT

Spawning occurs from late May into July but mainly in a 3-wk period from late May to mid-late June. Spawning ends progressively later proceeding upstream. Light intensity seemed to regulate when spawning began each day. Fish selected shallow riffle areas in preference to pool habitat for spawning. Spawning behavior is described.

Except for the most grossly polluted tidal water, spawning and nursery areas now extend throughout fresh water of the main Delaware and into the East and West branches. The most important spawning grounds and nurseries are now located from Port Jervis, N.Y., to Hancock, N.Y., and extend into the lower East Branch; this has probably been the case since 1910-20. There has been a fundamental upstream shift in the chief spawning grounds and nurseries since the decline of the Delaware River shad runs, because these historically extended downstream from about Delaware Water Gap, Pa., and included tidal water. Reasons for this shift suggest intrastream homing.

Only a small proportion of the historical nursery now contributes to production. Nursery and spawning areas now contribute to production of adults in proportion to their distance from Philadelphia, Pa. The extent of the spawning and nursery area since about 1910-20 has probably expanded and contracted around a core area in the upper Delaware near Hancock. Future prospects of Delaware River shad are discussed. They depend upon water quality in the tidal area and the proposed Tocks Island dam. Extirpation of the remnant runs is a distinct possibility.

The Delaware River basin once supported larger landings of American shad, *Alosa sapidissima*, than any other river system (Stevenson 1899). Annual landings near the turn of the century averaged about 14-17 million pounds but have consistently been much less than 0.5 million pounds since 1920 (Sykes and Lehman 1957; Chittenden 1974). Gross pollution near Philadelphia, Pa. (Figure 1), has been the chief reason for the low abundance since at least 1920 (Ellis et al. 1947; Sykes and Lehman 1957; Chittenden 1969). If pollution were cleared up, shad runs could be largely restored (Chittenden 1969).

Spawning and nursery areas of shad in the Delaware River are not well known, although the U.S. Army Corps of Engineers proposes to construct a dam near Tocks Island, a few kilometers upstream of Delaware Water Gap, Pa. If proposed fishways are not successful, this dam would prevent access to nearly half the 406 km of fresh water between Marcus Hook, Pa., and Hancock, N.Y. Sykes and Lehman (1957) concluded that the chief spawning and nursery areas were located upstream of Tocks Island. Their studies were made in 1950-52 when shad runs were almost nonexistent, however, and their conclusion was necessarily based on extremely limited data. Shad runs markedly resurged during the early mid-1960's when I made extensive collections and observations of adults and young. This paper describes the spawning period, behavior during the spawning period, recent and historical spawning and nursery grounds, and discusses the future prospects of shad in the Delaware River.

MATERIALS AND METHODS

Locations referred to are indicated in Figure 1 or, when first mentioned, by their approximate distances upstream from Marcus Hook, situated about 90 km downstream from the fall line at Trenton, N.J., and near the transition between fresh and brackish water.

Adults (278 males and 250 females) were collected during the spawning runs at Lambertville, N.J., using a 76-mm stretch-mesh, 107-m long and 3.6-m deep haul seine at 3- or 4-day intervals from 5 April to 19 May 1963, 20 March to 18 May 1964, 26 March to 7 May 1965, and 27 March to 19

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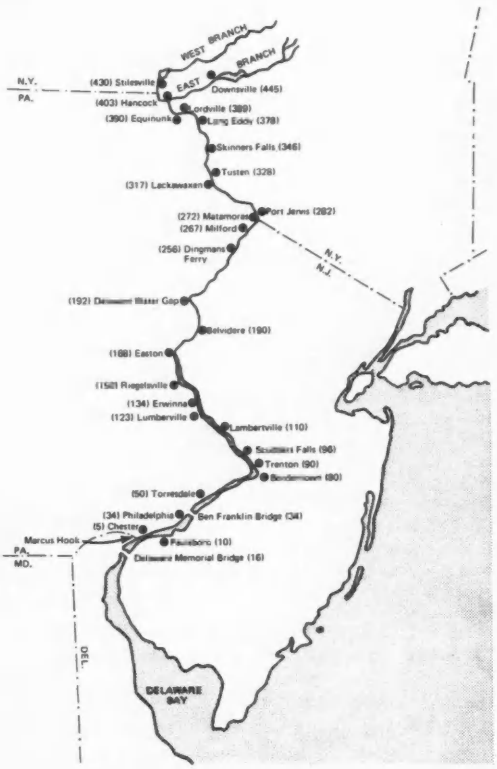

FIGURE 1.—The Delaware River. Numbers in parentheses represent distance in kilometers from Marcus Hook, Pa.

May 1966. Low dissolved oxygen near Philadelphia blocked upstream passage of part of the 1965 spawning run, and few fish were captured at Lambertville (Chittenden 1969); however, 43 dead males and 147 females were collected 21 May-10 June during a fish kill near Paulsboro, N.J. The gonads of all adults collected were examined to assess their degree of maturation following criteria of Leach (1925).

Data on the abundance of adults in the period 1959-62 were obtained from surveys (hereinafter referred to as the Tri-State Surveys) during July and August by the states of New Jersey, New York, and Pennsylvania in cooperation with the U.S. Fish and Wildlife Service. Rotenone was used to collect. After 1962 I made many observations on adult abundance and gonad condition during irregular collections upstream from Dingmans Ferry, Pa., especially during annual float trips in late May between Hancock and Port Jervis, N.Y. Observations on behavior during the spawning period were made chiefly in the East Branch near Hancock.

Young fish were collected in nontidal fresh water from 1963 to 1966 using 12-mm stretch-mesh seines. In 1963, most collections were made from Milford, Pa., upstream into the East and West branches using a 1.8-m deep, 6-m long net or a similar 10.7-m long bag seine. Most seine hauls in 1963 captured few or no young, but a few hauls captured many fish. Quantitative comparisons of abundance were considered unreliable because of the extremely contagious fish distribution. Therefore, techniques were greatly modified in 1964. A 22.9-m long, 1.8-m deep net was paid out from a pram. Lights (900 W for 1 h) were used at night to attract young shad to the shoreline for most collections during 1964 and thereafter. Only one seine haul was made at a station when lights were used, and collection sites were near deep water.

During 1966, night seining with lights was conducted at 2-wk intervals at Lordville, N.Y., Tusten, N.Y., Dingmans Ferry, Belvidere, N.J., Riegelsville, Pa., and Scudders Falls, N.J., from 1-4 August to 27-29 September and weekly thereafter until 14 November following an unreplicated two-way (stations and collections periods) experimental design in which collections were made at each station until the young completely vacated nontidal water. No F tests for significant differences in abundance were possible because of the inherent nature of the study: collecting with lights made catches reliable but replication impossible; intensive seaward movement of the young by mid-late August caused a stations by collection period interaction which negated tests for main effects. Supplementary collections using lights were made during 1966 in the East and West branches and downstream from Dingmans Ferry (Table 1).

Nurseries refer herein to areas the young occupy during July and August. Data for 1963, 1964, and 1966 (after August) are presented in Chittenden (1969, tables 35, 36, 38, 39, 41).

SPAWNING PERIOD

Nearly all spawning apparently occurred within a 3-wk period from about late May to mid-late June, although some spawning extended well into July. No fish had any translucent eggs until early May at Lambertville, and only one running

TABLE 1.—Summary of catch size (n) and total lengths (mm) of young American shad collected during July and August 1966.

Date	Location	n	Mean	SD	Min	Max
July						
5	Dingmans Ferry[1]	129	37.8	5.30	26	51
6	Belvidere	46	40.4	7.09	32	60
7	Scudders Falls	7	41.0	10.28	28	53
17	Erwinna	0	—	—	—	—
25	Riegelsville	12	51.2	8.39	42	71
25	Scudders Falls	3	68.3	8.50	60	77
August						
1-4	Lordville	208	37.1	4.57	27	52
1-4	Tusten	516	43.5	9.22	26	80
1-4	Dingmans Ferry	193	62.1	9.67	34	82
1-4	Belvidere	83	62.9	8.19	48	90
1-4	Riegelsville	8	62.9	10.86	49	78
1-4	Scudders Falls	0	—	—	—	—
7	East Branch, Hancock[1]	406	—	—	—	—
7	Downsville	0	—	—	—	—
8	Fishs Eddy	2	44.0	4.24	41	47
8	West Branch, Hancock	0	—	—	—	—
15-17	Lordville	363	46.6	9.21	26	79
15-17	Tusten	367	50.6	7.51	34	76
15-17	Dingmans Ferry	1,282	67.5	8.79	42	93
15-17	Belvidere	177	65.9	8.55	46	98
15-17	Riegelsville	16	74.3	10.14	47	90
15-17	Scudders Falls	12	94.8	8.70	82	109
29-31	Lordville	526	53.4	8.64	34	86
29-31	Tusten	45	62.1	9.95	44	87
29-31	Dingmans Ferry	124	70.7	8.80	54	100
29-31	Belvidere	63	75.3	8.61	62	97
29-31	Riegelsville	1	55.0	—	55	55
29-31	Scudders Falls	0	—	—	—	—

[1]The listed n was estimated as about half the total catch; large amounts of detritus were mixed with the East Branch, Hancock catch, small fish were hard to find and measurements were not taken.

ripe female was captured as early as 15 May. The gonads of some dead fish collected near Marcus Hook on 21 and 23 May 1965 were nearly ripe. Three females seined at Skinners Falls, N.Y., on 3 June 1964 had partially spawned. In the East Branch near Hancock, I observed much spawning from 10 to 17 June 1964; a few adults moved into a spawning area there after dark on 1 July 1965, suggesting that some spawning occurred then. Most spawning probably occurred before late June, however, because there was a great mortality of adults by then (Chittenden 1976).

Spawning ended at a later date upstream than it did downstream based upon the minimum sizes of young captured (Table 1). Assuming a month between hatching and transformation at about 25 mm (Walburg and Nichols 1967), spawning in 1966 ended about 7 June near Scudders Falls and about 25 June near Riegelsville. At Belvidere, spawning occurred at least until early June and at Dingmans Ferry until 1 July. Spawning ended near Tusten from 1 to 15 July and at Lordville from 15 July to 1 August. Length frequencies of young in July and August 1966 (Chittenden 1969) also show that spawning ended later upstream than it did downstream. However, the spawning period probably varies slightly between years and at different locations depending upon spawning stimuli.

The spawning period is apparently prolonged for individual fish. The ovaries of females captured near Hancock during June 1964 varied in size, many ovaries being about one-third or two-thirds the size of those from prespawning fish captured at Lambertville. This suggests prolonged spawning of individuals as Lehman (1953) concluded from egg diameter measurements.

BEHAVIOR DURING THE SPAWNING PERIOD

During the day, behavior depended upon the habitat occupied. The nontidal Delaware consists of a sequential arrangement of shallow swift riffles and slow-moving deep pools. Shad preferred pools but were frequently observed in riffles about 0.3 m deep. Schools of fish circled slowly in the pools but often formed a V in riffles. The point of the V headed upstream or in the direction of travel and left a readily observed wake. When the school was stationary and facing upstream, the fish at the point of the V moved to the rear after about 30 s. The fish immediately behind these leaders then moved to the point. This behavior spreads energy expenditure among all members of the school and may conserve energy as would the preference for pools. Both may be important to survival. Weight loss during the spawning migration is high (Leggett 1972; Chittenden 1976), and starvation causes a large mortality on the Delaware River spawning grounds (Chittenden 1976).

Adults were observed after dark in the shallows by using a pole to suspend a lantern high in the air. The large schools typical of the day seem to disperse during the evening spawning period, because only one to three fish were usually observed. Several times a behavior was observed which may have been the spawning act: a smaller fish (male?) lined up on either side of a larger fish (female?) bringing their vents in close proximity while swimming; a brief splashing coincident with a rattling sound occurred at or near the surface; and the fish separated after a few seconds. Splashing and rattling noises were continually heard outside the lighted area. This behavior was only witnessed after dark, and it occurred in water as shallow as about 150 mm. Plankton nets were not available to collect fresh eggs to confirm

this was the spawning act. However, the vigorous splashing and noise is similar to the observations of Goode (1888) and Leach (1925) and of Leim (1924) who used plankton nets to collect newly fertilized eggs.

Light intensity seemed to regulate when spawning began each day, and the shad seemed to prefer shallow riffle areas for this activity. Few fish were observed during the day in a shallow riffle spawning site near Hancock, but many fish moved from the upstream pool to the riffle as evening approached. Concentration near the riffle occurred earlier on overcast days than on sunny days. I observed spawning only at night in general agreement with Pennsylvania (1875), Goode (1888), Leim (1924), Leach (1925), Walburg and Nichols (1967), and Marcy (1972). In contrast, Massmann (1952) found spawning at all hours in the Pamunkey River, Va., although possibly more intensively from noon to midnight. Water turbidity probably influences the effect of light in regulating the daily onset of spawning. Spawning probably tends to occur at night in clear water such as the upper Delaware, but seems to begin later during the day or occurs all day long in turbid water typical of tidal areas such as the Pamunkey River. Overcast skies apparently permit spawning to begin earlier in the day.

SPAWNING GROUNDS

Important spawning grounds apparently extend no farther downstream than the Belvidere area. During the Tri-State Surveys, greatest numbers of adults were captured from Minisink Island to Skinners Falls, and none were captured downstream from Manunka Chunk (Table 2). Few adults were captured from Long Eddy, N.Y., upstream. However, these collections were made 10-21 July which is well after most adults move seaward or die (Chittenden 1976). Therefore, the chief spawning grounds may have been farther upstream.

Extensive observations from 1962 to 1968 generally support the Tri-State Survey collections, but in contrast they suggest that the area from Skinners Falls to the lower East Branch was extemely important. Many adults were observed 31 May-1 June 1962 from Milford to Delaware Water Gap, and 30 May-5 June 1963 from Mongaup River (km 296) to a few kilometers above Callicoon, N.Y. (km 360). In 1964, hundreds of adults were observed near Hancock and the lower East Branch 29 May-20 June and (J. Musick pers. commun.) near Milford on 31 May. Fewer adults were observed after 1964, but they consistently appeared from Sparrowbush, N.Y. (km 286), to the lower East Branch in late May and early June.

TABLE 2. — Numbers of adult American shad captured during the Tri-State Surveys.

Station	Distance from Marcus Hook, Pa. (km)	1959	1960	1961	1962
East Branch, Hancock	403	0	0	5	—
West Branch, Hancock	403	0	0	0	—
Long Eddy	378	0	0	23	—
Skinners Falls	346	0	11	107	134
Mongaup Area	292	0	0	271	—
Minisink Island	263	30	0	160	103
Tocks Island	218	0	0	0	0
Manunka Chunk	197	—	32	40	—
Raubs Island	152	—	0	0	—
Marshalls Island	132	—	0	0	0
Scudders Falls	95	—	—	0	—
Trenton Falls	88	—	—	—	0

Some spawning occurs downstream of Philadelphia; however, few fish which pass Philadelphia spawn as far downstream as Lambertville. I collected a nearly spent male on 10 June 1965 at Marcus Hook. This fish undoubtedly had spawned nearby, because low dissolved oxygen would have prevented movement past Philadelphia after April (Chittenden 1969). The Lewis Fishery at Lambertville captured about 6,300 fish from 1963 to 1968, but only 21 were taken after 15 May.

Spawning extends into the lower West and East branches, especially the latter, but dams prevent movement upstream of Stilesville, N.Y., and Downsville, N.Y. Young shad (27 mm total length) were captured in the West Branch at Hancock on 9 August 1963 (Chittenden 1969, table 26). This suggests spawning there because net movement of the young is downstream. Adults were collected in the East Branch at Hancock during the 1961 Tri-State Surveys. Many occurred at least as far upstream as East Branch, N.Y. (km 430), in the runs of 1962-65 (W. Kelly pers. commun.; my observations). I observed spawning in the East Branch near Hancock in 1964 and 1965.

The adults ascend some tributaries, but it is not certain if they spawn there. A female was caught on 16 May 1961 in Big Flat Brook (km 235) about 10 km upstream from the Delaware (Anonymous 1961). Adults ascended several kilometers up the Mongaup River from 1962 to 1964 and 6 km up the Beaverkill River, an East Branch tributary (W. Kelly pers. commun.).

NURSERIES

The chief nursery in 1966 was apparently located upstream from Dingmans Ferry and was especially centered near Tusten and Lordville (Table 1). Areas downstream from Tusten gradually decreased in relative importance. The chief nursery extended into the lower East Branch; many young were captured near Hancock on 7 August, but none were taken at Downsville and few were collected at Fishs Eddy, N.Y. No fish were captured in the West Branch near Hancock on 8 August, suggesting that the lower West Branch was an unimportant nursery in 1966.

Two seemingly aberrant catches affect interpretation of relative abundance upstream from Belvidere. The catch was small at Tusten on 30 August and very large at Dingmans Ferry on 17 August. Hundreds of young were attracted to the lights on 10 and 21 August at Tusten which agrees with the magnitude of catches on 4 and 16 August. The Tusten catch on 30 August probably reflects a seaward exodus of fish after 21 August. A plateau in size formed at Tusten by August 30 (Chittenden 1969, figure 47) when mean total length was 62 mm (Table 1). A plateau represents seaward movement of larger fish, and seaward movement of the young is probable when they reach 64 mm (Chittenden 1969:248). Mean size at Dingmans Ferry was 62 mm on 4 August and 67 mm on 17 August, so that the very large catch at Dingmans Ferry on 17 August probably reflects an influx of seaward moving young from farther upstream.

The Delaware River downstream of Belvidere appears to be a relatively unimportant nursery. Catches during July and August 1966 at Riegelsville and Scudders Falls were consistently much smaller than at stations farther upstream, and a catch at Erwinna, Pa., in July was also small. The largest catch in these 10 collections was 16 young. This is much smaller than the smallest catch in 14 collections at Belvidere, Dingmans Ferry, Tusten, and Lordville.

My collections and observations in 1963-65 generally agree with the nursery patterns of 1966. In 1963, young shad were observed and captured from Dingmans Ferry to the lower East and West branches; many were repeatedly observed and collected in the lower East and West branches at Hancock, and hundreds were observed near Matamoras, Pa., on 19 July and at Skinners Falls on 30 August. In 1964, young were captured from Erwinna upstream to Cochecton, N.Y. (km 354): hundreds were observed or captured at Belvidere, Delaware Water Gap, Worthington Tract (km 217), Flatbrookville (km 235), Dingmans Ferry, Sparrowbush, Pond Eddy (km 301), and Cochecton. No collections were made upstream from Cochecton in 1964 except on 18 August when no young were captured using lights in the West Branch at Hancock. In 1965, young were observed or captured from Belvidere upstream to Pond Eddy; hundreds were observed and captured at Delaware Water Gap on 8 July, at Belvidere on 15 July, and at Dingmans Ferry, Sparrowbush, and Pond Eddy on 21 July. No trips were made upstream of Pond Eddy in 1965.

GENERAL DISCUSSION

Historical Spawning and Nursery Areas

Shad migrated 68 km up the East Branch to Shavertown (Bishop 1936) and 24 km up the West Branch to Deposit in the early 1800's (Gay 1892). A dam constructed at Lackawaxen, Pa., however, blocked access upstream after 1823 (Slack 1874; Smiley 1884; Gay 1892). Spawning grounds then extended downstream from Lackawaxen for about 70 yr until a fishway permitted upstream access in 1891 (Bean 1892, 1903).

Apparently the chief spawning grounds were historically downstream from Lackawaxen. The shad catch along the Atlantic coast is primarily age IV or older fish (Walburg and Nichols 1967). Few Delaware River shad migrate upstream until age III, and most now first do so at ages IV and V (Chittenden 1975). No records exist of size or age composition in the late 1800's-early 1900's when Delaware River landings reached their zenith, except that average weights about 1896 were 3.75 and 3.50 pounds (Stevenson 1899), 3.75 pounds (Townsend 1901), and 4.2 pounds based upon Smith's (1898) report on the numbers and pounds caught. These weights are reasonably similar to the mean weights of males (1,107 g) and females 1,737 g) captured at Lambertville from 1963 to 1965 (Chittenden 1976), so that recent Delaware River data probably closely represent the age structures near the turn of the century. Therefore, renewed access to spawning grounds upstream from Lackawaxen could not have fully affected landings until 1895 or 1896. Except for 1892, annual landings were about 13-14.5 million pounds in the period of 1889-95 and about 13.9-16.8 million pounds from 1896 to 1901 (Chitten-

den 1974). The catches in these two periods are so similar that it would appear that the Lackawaxen Dam had little effect on abundance. The chief spawning grounds may have been located even further downstream than Lackawaxen, however, because Abbott (1868) stated that shad were seldom plentiful upstream from Delaware Water Gap, and this is supported by Smiley's (1884) statement that no shad were seen farther upstream than Milford for 25 yr prior to 1872. Shad were abundant at that time (Slack 1874).

Spawning grounds could have extended downstream to about Marcus Hook, because shad spawn in fresh water (Prince 1907; Leach 1925; Hildebrand and Schroeder 1928; Massmann 1952). Consideration of preferred spawning and nursery habitat and Delaware River morphology suggests that tidal water was historically important: the existence of an extensive tidal nursery (and spawning area) immediately downstream from extensive excellent spawning grounds was probably important to the former abundance of Delaware River shad (Chittenden 1973b). However, the contemporary literature conflicts on the importance of the tidal Delaware (Pennsylvania 1897; discussion session after Meehan 1907; New Jersey 1916).

The potential importance of the tidal Delaware can be judged by comparison with other rivers. Hudson River runs are entirely produced in tidal water, because a dam constructed in 1840 at Troy, N.Y. (Cheney 1896), blocks passage of shad to nontidal water. Annual Hudson River landings were 2-4 million pounds from 1936 to 1949 and catches of about 5 million pounds have been reported (Talbot 1954). Migration of shad in the Potomac River is blocked by Great Falls, 16 km upstream from tidal water, so that most fish are probably from tidal spawning. Spawning grounds in several Virginia rivers are in tidal waters (Massmann 1952). Therefore, it appears that tidal spawning was once very important in the Delaware River, in agreement with Walford [a 1951 memorandum cited by Mansueti and Kolb (1953)] who stated that the principal spawning area once was probably a short distance above Gloucester, N.J. (km 30).

The area near Hancock apparently became an increasingly important spawning area—but eventually for reduced numbers of fish—as the Delaware River shad runs declined. Many fish again moved upstream into the East Branch after installation of the Lackawaxen fishway in 1890 (Bean 1892, 1903). Landings from 1904 to 1913, in general, were only about 3-5 million pounds and consistently have been much less than 0.5 million pounds since 1920 (Sykes and Lehman 1957; Chittenden 1974). In spite of this great decline, many shad (240-350/seine haul) were captured at Hancock until 1915 (Bishop 1936). Catches near Hancock gradually declined after 1915, and a shad fishing club captured only 60-75 fish annually after 1920 and less than 12 in some years (Greeley 1936; Bishop 1936).

Many tributaries, particularly in the tidal area, may have been used for spawning and as nurseries; but their historical importance is not clear. Adults entered many tributaries near Philadelphia (Meehan 1896; Stevenson 1899). The Lehigh and Schuylkill rivers were once famous shad streams (Gay 1892; Meehan 1896), although dams were constructed after 1820 and prevented access to these streams.

Recent Spawning and Nursery Areas

With the probable exception of the most grossly polluted tidal areas, recent spawning and nursery areas have extended throughout fresh water of the Delaware and into the East and West branches. In general, nurseries must be at or downstream of spawning grounds, because the young begin to disperse downstream upon transformation from the post-larval stage—if not sooner (Chittenden 1969).

The chief spawning grounds and nurseries now extend no farther downstream than Belvidere. Gonad condition, the presence of few adults after mid-May, and the location of the chief nurseries, especially during early July, indicate that very little spawning occurs as far downstream as Lambertville. The Delaware between Belvidere and Philadelphia probably now serves as a nursery primarily due to downstream dispersal of the young. The importance of spawning grounds and nurseries now increases proceeding upstream from Belvidere towards Hancock. The most important spawning grounds and nurseries are located from about Port Jervis to Hancock and extend into the lower East Branch.

Tidal water near Philadelphia is no longer suitable as a nursery and probably not for spawning. Although conditions vary slightly between years, in general, the minimum daily dissolved oxygen is at or near 0 mg/liter from about mid-May through early December in the 66-km

stretch from Torresdale, Pa., to the Delaware Memorial Bridge, the most severely affected area being from Chester, Pa., to the Benjamin Franklin Bridge (Chittenden 1969). Minimum daily dissolved oxygen levels of about 2.5-3.0 mg/liter are needed to permit mere survival of shad, and this is not a reasonably normal existence (Chittenden 1973a).

Some spawning probably occurs in fresh water seaward of Philadelphia when low oxygen prevents upstream passage of part of the run. Therefore, this area would be a nursery. The area is limited in extent, however, and survival of fish may be precarious because of daily dissolved oxygen fluctuations due to photosynthesis or tidal movement of polluted water. de Sylva et al. (1962) collected larval shad, but no juveniles, in the Delaware River estuary shore zone even though the euryhaline young can and do utilize brackish nurseries (Chittenden 1973b). Production of shad seaward of Philadelphia, at best, apparently is small because landings in the Delaware Basin have been low for more than 50 yr.

The West Branch is apparently no longer an important nursery. Young shad were repeatedly collected at Hancock in 1963, but none were captured in two collections with lights in 1964 and 1966. Cold water releases from Cannonsville Reservoir, which began after summer 1963, may account for the apparent absence of young in the West Branch thereafter (Chittenden 1972). If so, the East Branch and possibly the Delaware below Hancock may be of precarious suitability for spawning and nursery purposes, because Pepacton Reservoir on the East Branch is also designed for water release from the hypolimnion.

Tributaries act as nurseries and possibly spawning grounds but are probably not important to production today in the Delaware River. Compton (1963) captured 38 young on 23 July 1962 in Big Flat Brook, nearly 1.6 km from the Delaware, and adults have been observed in several tributaries. Tributaries in nontidal water are too small to support many fish, however, except for the Lehigh River (km 168) which is dammed near its junction with the Delaware. Those in tidal water near or upstream of the Philadelphia area are dammed, affected by tidal movement of low oxygen water, or the young produced therein reach Philadelphia too early in summer or fall to successfully pass seaward (Chittenden 1969).

The present findings on spawning and nursery areas agree with Sykes and Lehman's (1957) observations and with their descriptions of unpublished findings of Cable: plankton tows were taken in May 1944 from Bordentown, N.J., to Equinunk, Pa.; the greatest concentration of eggs was above Lackawaxen and no eggs were found below Lumberville, Pa. Therefore, it would appear that the chief spawning grounds and nurseries have remained about the same for at least the last 30 yr and probably since about 1910-20.

Areas Contributing to Successful Production of Adults

It appears that there has been a fundamental shift in the chief spawning grounds and nurseries since the decline of the Delaware River shad runs. Historically the chief spawning grounds were downstream of Delaware Water Gap and included the tidal area. These areas are now of little importance; since the decline, the chief spawning grounds have been upstream of Delaware Water Gap. The most important spawning grounds and nurseries for the last 60 yr or more have seemingly been near the Hancock area.

Implications of the shift in spawning and nursery areas include the existence of an intrastream homing tendency which brings the fish back to spawn in their general area of birth. Chittenden (1969) discussed in detail causes of the decline in abundance of Delaware River shad and why abundance has remained low. I suggested (1969:424) that the shift in spawning and nursery areas occurred because pollution near Philadelphia has selected for an upstream-spawning stock based upon the time when the young reach the Philadelphia area; fish produced farthest downstream have the greatest probability of reaching Philadelphia before dissolved oxygen improves sufficiently to permit successful seaward passage. This implies intrastream homing. Interstream homing exists in shad (Hammer 1942; Hollis 1948; Talbot and Sykes 1958; Nichols 1960), but direct evidence of intrastream homing is desirable.

Spawning and nursery areas near Hancock are apparently the key to maintenance of the remnant Delaware River shad runs, because Chittenden (1969) demonstrated that the last fish to move seaward were, in general, those produced farthest upstream. The extent of the spawning and nursery area since about 1910-20 or earlier has probably expanded and contracted depending upon the size of the run and spawning success.

Important spawning and nursery areas probably extend farthest downstream when the run is large and spawning is successful. The upper Delaware area near Hancock is probably the core around which expansion and contraction occurs.

Downstream sections of the nursery usually contribute little or nothing to production of adults even if the nursery expands. Since 1925, larger shad runs in the Delaware River have depended upon one year class which successfully passed the Philadelphia area (Chittenden 1975). Downstream nurseries contribute to production only when water quality near Philadelphia permits shad passage earlier than normal; there is usually catastrophic destruction of the young as they pass Philadelphia (Chittenden 1969). Therefore, in general, it appears that nursery and spawning areas contribute to production in proportion to their distance from Philadelphia. Only a small part of the historical nursery area now contributes to production of adults.

Future Prospects

Future prospects of shad in the Delware River depend primarily upon water quality in the tidal area and upon a dam near Tocks Island (Chittenden 1969). The present remnant runs appear based upon stocks that spawn far upstream in a small part of their former spawning grounds and whose progeny pass tidal water in late fall when dissolved oxygen increases. A greater area would contribute to successful production if dissolved oxygen increased earlier, because fish spawned farthest downstream pass tidal water first. Therefore, the magnitude of future runs will reflect dissolved oxygen conditions, because the area contributing to production will change accordingly. If recent or typical water quality was maintained, future runs would usually be small. Fortuitous circumstances would occasionally produce larger runs as in the early 1960's.

Construction of a dam near Tocks Island would greatly affect shad. They probably would be extirpated from the Delaware if successful fishways for both adults and young are not provided and water quality in the tidal area is unchanged. Cold water reservoir releases drastically and adversely affect usage of downstream spawning and nursery areas, if only due to avoidance (Chittenden 1972). Cold water releases from a Tocks Island dam would shift spawning and nursery areas far downstream, and spawning grounds under any water release circumstances would be downstream of the area that presently produces adults successfully. Therefore, the young produced would reach tidal water too early to pass seaward successfully. Great water quality improvement would be needed in the tidal area just to maintain the present small runs. Water quality improvement by flow augmentation might be self-defeating, because the young now move downstream even during the summer; and increased discharge and temperature decrease would accelerate this. The potential would be brighter if successful fishways were provided. The reservoir might be an excellent nursery for the young judging from their pelagic habits, their preference for pool habitats, and the former importance of tidal nurseries. This, combined with nurseries upstream from the reservoir, might establish larger runs—if the young passed the dam and tidal water successfully. However, much larger runs would be achieved with less risk at possibly less cost if Delaware River water quality in the tidal area were restored and the dam was not built. Then, the outstanding recreational potential of a clean tidal area in a great population center would be restored—and the outstanding recreational opportunity of an unobstructed Delaware River would not be lost.

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LARVAL DYNAMICS OF THE DUNGENESS CRAB, *CANCER MAGISTER*, OFF THE CENTRAL OREGON COAST, 1970-71

R. GREGORY LOUGH[1]

ABSTRACT

The larval dynamics of the economically important Dungeness crab, *Cancer magister*, were investigated from plankton samples collected bimonthly during 1970 and 1971 along a trackline near Newport, Oreg. Larvae appeared at maximum densities (8,000/1,000 m³) within 15 miles of the coast in late January 1970 and remained in the plankton until late May for an approximate larval period of 130 days. The bulk of the larval population was retained in the nearshore area by the strong alongshore and onshore components of the surface currents and to some extent by the behavior of larvae in determining their position in the water column. During the 1971 season, larvae appeared initially at about the same time and densities, but a mass mortality may have occurred in the early zoeal stages coinciding with the unusually severe weather in February and March. A significant difference between the 1970 and 1971 larval populations was suggested by analysis of covariance using sea surface temperature and salinity as environmental variables. However, the effect of the low temperature and salinity values that occurred during the winter of 1971 were not clearly indicated by multiple regression analyses of laboratory experimental data to be the prime factors directly affecting larval survival. Neither did a gut-fullness study of planktonic larvae substantially explain the 1971 larval mortality. Therein various hypotheses are explored in view of the present knowledge of processes affecting larval survival and recommendations are suggested for further research.

It is well known that many species of economically important marine resources fluctuate greatly in number and location. These fluctuations may be explained in part by changes occurring in the larval populations. That the larval stage is the most critical period for the majority of marine animals was originally emphasized by Hjort (1914, 1926) for fish larvae and by Thorson (1946) for marine invertebrate larvae. Survival through this period is usually considered the major factor in determining the strength of the year class. The causes or extent of larval mortality, however, are still relatively unknown.

Bimonthly plankton samples were collected from 1969 through 1971 along a transect off the central Oregon continental shelf to document the species of crab larvae present, their seasonality and abundance, and their onshore-offshore distribution in relation to seasonal changes in oceanographic conditions (Lough 1975b). A major effort was made to assess the larval population of the Dungeness crab, *Cancer magister* Dana, as it supports one of the most important fisheries in the Pacific Northwest.

Cancer magister occurs along the Pacific coast from Unalaska to lower California and ranges from mean low water to 50 fathoms (91 m) (Schmitt 1921). Although it prefers sandy or sandy-mud bottoms of the nearshore area, specimens have been found on all bottom types within estuaries and on the continental slope. Adult females generally reach maturity by their second or third year and may produce three or four broods during a life-span (MacKay 1942; Cleaver 1949; Butler 1960). Egg-carrying females are found in Oregon waters from October to March with essentially one brood produced per year (Waldron 1958). Field observations (Waldron 1958) and laboratory rearings by Poole (1966) and Reed (1969) indicate that larvae hatch off northern California and Oregon from January through March and are present in the nearshore waters through July for a total estimated larval life of 128 to 158 days. *Cancer magister* passes through five zoeal stages and one megalops during its larval development before settling out of the water and metamorphosing to the benthic juvenile.

HYDROGRAPHIC FEATURES OF STUDY AREA

The surface waters along the U.S. west coast are dominated by the California Current; a slow,

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broad, and shallow current flowing equatorward (Wooster and Reid 1963). The nearshore currents vary seasonally and are dependent upon wind direction and strength. During the fall and winter months when the winds are predominantly from the southwest, a subsurface countercurrent flowing northward along the coast develops into the Davidson Current. Drift bottle studies by Wyatt et al. (1972), Burt and Wyatt (1964), and Schwartzlose (1964) indicate that the Davidson Current first develops along the Oregon-Washington coast in September reaching maximum speeds between 0.5 and 2 knots within 20 miles of the coast during the month of November.

The major change in the surface currents from northward to southward occurs in March and April (Wyatt et al. 1972). The phenomenon of coastal upwelling occurs when the northwesterly winds intensify and sometimes persist from May to September. As the surface waters are transported offshore and to the southwest, cold, high salinity waters from below a permanent pycnocline (60-100 m) are brought to the surface (Smith et al. 1966). This zone of active upwelling occurs within 20 miles of the coast but its effects can be observed to the edge of the slope.

The area within 5 miles of the coast has not been studied in much detail but is believed to be dominated by mixing processes (Mooers 1970). The surface currents are generally well correlated with the wind direction, but tidal currents predominate when the wind is reduced. A very strong alongshore current with an onshore component is indicated within 3-5 miles of the coast (Keene 1971; Wyatt et al. 1972; Holton and Elliot 1973).

The dominant processes modifying surface water properties off the Oregon coast during the winter are rainfall and river runoff; while during the summer, the major processes are upwelling in conjunction with heating and mixing with the Columbia River plume water (Pattullo and Denner 1965). Surface temperatures and salinities taken on early life history cruises from June 1969 through August 1971 at stations NH01-NH10 are presented in Figures 1 and 2. Temperatures range annually from about 7° to 17°C and are highest from May through October, peaking in September. More variability is evident during the summer due to surface heating interrupted by local upwelling of near 7°C bottom water. Surface salinity values are generally low during the winter and high in the summer reflecting seasonal precipitation and upwelling, respectively. The annual range of salinity is from about 25 to 35‰. Low salinity values at stations NH03 and NH05 from November through April are probably associated with the Yaquina Bay plume which flows north along the coast during the winter (Kulm and Byrne 1966).

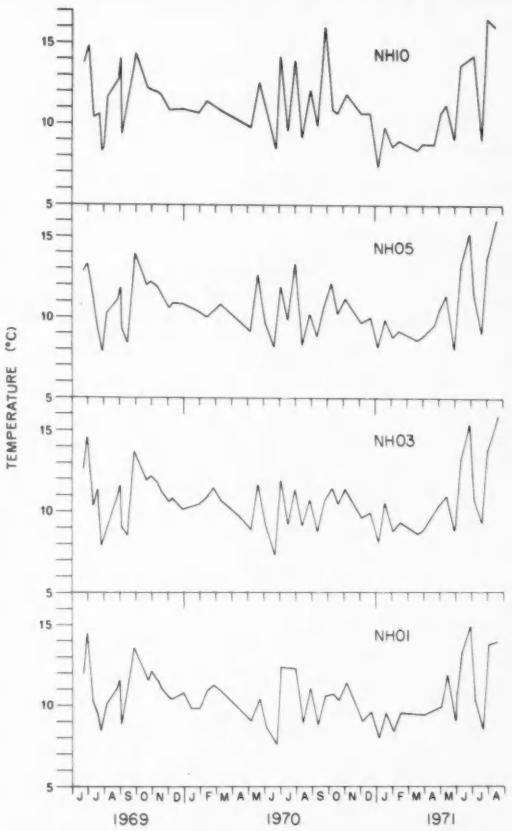


FIGURE 1.—Surface temperature (°C) at stations NH01, NH03, NH05, and NH10 from June 1969 through August 1971.

METHODS

Sampling Program and Gear

This study was conducted primarily on a trackline off Newport, Oreg. (lat. 44°39.1′N) across the continental shelf and slope. The 12 sampling stations are designated on the Newport Hydrographic line (NH) in Table 1, which correspond in distance to nautical miles from the

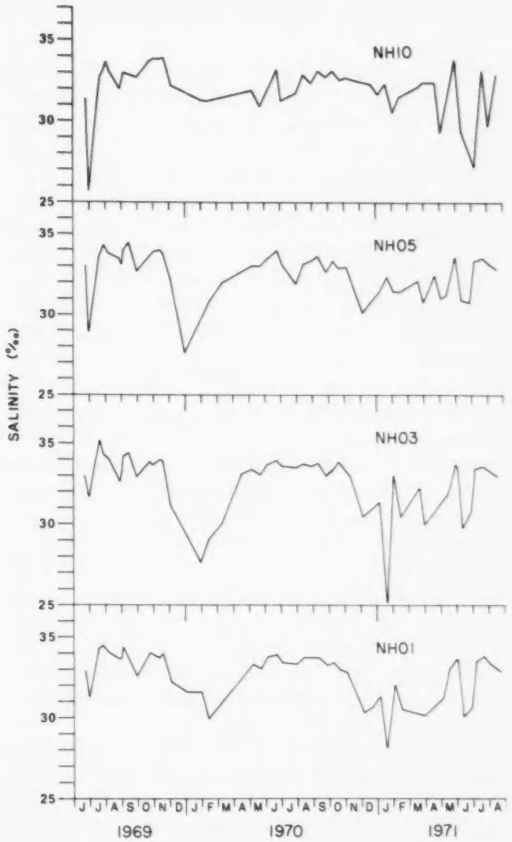


FIGURE 2.—Surface salinity (‰) at stations NH01, NH03, NH05, and NH10 from June 1969 through August 1971.

TABLE 1. — Location of plankton sampling stations and bottom depths along the Newport Hydrographic line (NH) off Newport, Oreg.

Station (Lat. 44°39.1'N)	Long.	Depth (m)
NH01	124°05.4'W	20
NH03	124°08.6'W	46
NH05	124°10.7'W	59
NH10	124°17.7'W	85
NH15	124°24.7'W	95
NH20	124°31.7'W	142
NH25	124°38.7'W	330
NH30	124°45.7'W	220
NH35	124°52.7'W	340
NH40	124°59.7'W	1,060
NH50	125°13.7'W	1,300
NH60	125°27.7'W	2,850

coast. Plankton samples initially were collected at the four inshore stations (NH01-NH10) constituting the main series of samples from June 1969 through August 1971. The sampling program was extended offshore to NH60 by 5- or 10-mile intervals beginning with the 3 February 1971 cruise.

A high-speed bongo net sampler (Posgay et al. 1968) with a 0.2-m mouth diameter was used exclusively from 22 June 1969 through 20 October 1970. The two cylinder-cone nets, 1.8 m in length, were constructed of 0.233- and 0.571-mm nylon mesh and had an effective straining surface (pore size area) to mouth area ratio of ca. 10 to 1. A 30-pound lead ball or a 15-pound V-fin depressor was attached to the sampler line.

Starting with the 4 November 1970 cruise, a 0.7-m diameter bongo net sampler was used in conjunction with the 0.2-m sampler to strain a greater volume of water and to reduce avoidance by the larger larvae. The 0.7-m bongo nets had a net length of 5.1 m, were constructed of 0.571-mm nylon mesh, and had an effective straining area ratio of ca. 8 to 1. Both samplers were equipped with TSK[2] flowmeters mounted on brackets 18 cm from the rim of the inside frame. A multiplane kite-otter wire depressor (ca. 80 pounds), modified after Colton (1959), was used with the dual bongo net array to produce a wire angle ratio of 2 to 1. The sampling objective was to make a high speed, oblique, plankton tow, sampling the water column in equal stepped intervals from 150 m depth, or in shallower areas from bottom to surface. Wire was let out and retrieved at 50-75 m/min while the vessel was underway at 2-3 knots. Most of the samples represent daylight (0600-1800) tows ranging in duration from 10 to 25 min. The longer tows were generally made on stations beyond 5 miles. Plankton samples were immediately preserved in 5-10% Formalin and later buffered with sodium borate.

A bathythermograph (BT) cast was made at each station near bottom or to 150 m depth. Surface bucket temperatures also were taken at each station to calibrate the BT readings. Salinity samples were collected on the surface and near bottom or to 150 m depth by a Nansen bottle cast and analyzed by an inductive salinometer. Salinity, temperature, and depth (STD) data from a real-time printout computer were available for several cruises.

The Nekton Cruise of 11-12 April 1970 at station NH45 was included in this study as it is one of the few cruises that sampled the offshore

[2]Tsurumi-Seiki Kosakusho. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

plankton during 1970. The objective of this cruise was to identify those organisms associated with sound scattering layers in the upper 150 m of seawater and, if possible, to follow their day-night migration patterns. Six successive integrated tows of approximately 45 min each were taken to a depth of 150 m (total time: 1852-2355). A standard 6-foot (1.8-m) Isaacs-Kidd mid-water trawl (IKMT) with a 2.9 m^2 mouth opening [1½-inch (3.8-cm) mesh with a ¼-inch (0.6-cm) linear nylon liner] was used for this series. The second series of eight samples alternately sampled from surface to 150 m and from 150 m to surface with an eight-bar electronic multiple plankton sampler (EMPS) attached to the IKMT (Pearcy and Mesecar 1970) (total time: 0134-0514). The cylinder-cone nets were approximately 2.9 m in length with a mouth diameter of 0.4 m and made of 0.571-mm nylon mesh. Another series also used the EMPS to sample eight discrete layers from the surface to 330 m depth covering three bands of scatters (total time: 0640-1113). Scattering layers were located using 12 and 38.5 kHz echo sounders. One automated STD cast was made.

Processing of Plankton Samples

Samples from both mesh sizes of the 0.2-m bongo nets were processed for the nearshore area, stations NH01-NH10. Only one side of the 0.7-m bongo net sampler was processed to examine the offshore area, NH15-NH60. Generally, the entire sample was sorted, however, many required subsampling using an 8-cm diameter plankton splitter (Longhurst and Seiburt 1967). Approximately 22% of the 0.2-m bongo net samples and 39% of the 0.7-m bongo net samples required subsampling. Those samples which required splitting were usually from stations NH01 and NH03.

All crab larvae were removed from the samples and positive identification of *C. magister* larvae was made from the descriptions given by Poole (1966) and from preserved specimens reared by Thomas F. Gaumer, Fish Commission of Oregon, Marine Laboratory, Newport, Oreg. Catches of larvae were first converted by computer to number per 1,000 m^3 of seawater and ordered in a format. Graphs of stage density against time were plotted for the 0.2-m bongo net samples, 0.571-mm mesh, with the aid of a CalComp plotter using the Oregon State University CDC3300 computer.

SAMPLING VARIABILITY

The detailed analyses of the various methods by which sampling variability affected the estimates of larval crab abundance are given by Lough (1975b). Variability estimates and sampler comparisons were made in this study on other species of crab larvae than *C. magister* for the most part, as limited ship time and weather played an important role in determining the objectives and priorities of the sampling program. Analysis of variance techniques were used to estimate the variance of a single observation in the manner of Winsor and Clarke (1940). Confidence limits for a single observation of either sampler usually exceeded the 50-200% range reported by Winsor and Clarke due to the relatively low densities of crab larvae sampled during replicate tows. A range of an order of magnitude was considered necessary to distinguish a real difference between any two observations. There was no significant difference between the total number and kinds of crab larvae caught by the two sides of the different sized samplers. The 0.7-m bongo net sampler gave smaller confidence limits for larval crab catches and was much superior in establishing significant differences between stations than the 0.2-m bongo net sampler.

Most of the nearshore samples (NH01-NH10) were taken during daylight hours; only 8.6% of the 0.2-m bongo net samples were taken at night between 1800 and 0600 h. More (26.7%) of the 0.7-m bongo net samples sorted beyond NH10 were collected at night. Most larvae were caught more abundantly in night tows than day tows for both sized samplers. Day-night differences in larval abundance were greater for the 0.2-m sampler than the 0.7-m sampler. There was a nearly equal distribution in the number of kinds of crab larvae caught between day and night samples using the 0.7-m sampler; however, using the 0.2-m sampler, significantly more kinds of larvae were caught at night.

The results of the Nekton Cruise showed that the larvae of *C. magister* occur in relatively low densities offshore as far as station NH45 during early April 1970. They are most likely to occur in the surface waters above 120 m, the depth of the thermo- and halocline and are probably associated with the first sound scattering layer at 25 to 90 m depth. A Mann-Whitney two sample rank test (Tate and Clelland 1957) retained the null hypothesis that there was no significant dif-

ference between the number of *C. magister* megalopae, or the total number of larvae caught in the first two series of tows. In the second series of samples more larvae were caught towing from surface to 150 m than from 150 m to surface and the total number of larvae decreased with time (0134-0514) for both alternate types of tows. The coefficients of variation (standard deviation/mean) for the total number of larvae were about the same for the first two series of tows (1.25 and 1.31, respectively) indicating a somewhat patchy distribution of the larvae in the upper 150 m of water at night. Very few larvae were caught during the third series of tows.

RESULTS

Distribution and Abundance of *Cancer magister* Larvae

Two larval seasons were encompassed by the sampling program (Figure 3). Zoea 1 larvae made their first substantial appearance during the first season on 29 January 1970 at stations NH03, NH05, and NH10 with maximum densities ranging from 1,000 to 3,000/1,000 m^3. The subsequent zoeal stages were found most abundantly at stations NH05 and NH10. Few zoea 4 and no zoea 5 stages were found at any of the four inshore stations. In general, the number of larvae captured decreased from zoea 1 through 5. However, large numbers of megalopae were found at stations NH01, NH03, and NH05, suggesting a general inshore transport of larvae during this season. Maximum densities of the magalopae ranged from 1,000 to 8,000/1,000 m^3, densities comparable to those of the zoea 1 stage found earlier in the year. Few megalopae appeared in the water column after 22 May 1970 and none after 16 July 1970. This indicates that the length of the larval period in the plankton is approximately 130 days (89-143 days). The summer upwelling conditions did not appear to have any effect on the larvae since the bulk of the megalopae had settled before the onset of intense upwelling.

The major appearance of zoea 1 larvae during the second season occurred at about the same time (18 January 1971) and stations (NH03, NH05, NH10), and at about the same densities (1,000-2,000/1,000 m^3). However, the density of the larvae appeared to decrease more rapidly at zoeal stages 2 and 3, and virtually no larvae of any stage were found after zoea 3. The 30 March 1971 cruise was the last sampling period which caught any significant number of larvae. Very few megalopae were found at any station throughout the summer in day or night samples.

Cancer magister was the most abundant crab larvae caught at station NH45, 11-12 April 1970 (Nekton Cruise). Its megalopae had the highest densities of any larval stage with 19/1,000 m^3, followed by zoea 5 at 12/1,000 m^3. Fewer zoea 4 and 3 were present. Scattered occurrences of all larval stages were present the following year, 1971, to 60 miles offshore in the 0.7-m bongo net samples. Megalopae and zoea 3-5 predominated offshore with densities usually much less than 200/1,000 m^3, suggesting that these larvae had originated nearshore and subsequently drifted offshore. Larvae present at stations NH35 to NH60 are under the influence of the Columbia River plume as indicated by the warmer temperatures and lower salinities measured at these stations during the sampling period.

All observations indicate a dramatic difference in the abundance of megalopae between the 2 yr. Sampling was much more intensive during the 1971 season from the standpoint of day-night replicate tows using both size samplers in the inshore and offshore areas when the megalopae were sparse.

Climate and Hydrography 1970-1971

The winter of 1971 along the Oregon coast was generally more severe than that of 1970. Climatological records (U.S. Environmental Data Service 1970,1971) for Newport and other ports of Oregon show monthly mean air temperatures for February and March 1971 to be substantially lower than the same months during 1970. Also, total precipitation generally was greater during the winter of 1971 but showed considerable variability along the coast. Ocean surface temperatures correspondingly were much colder during this period in 1971 than 1970. Gonor et al. (1970) and Gonor and Elvin (1971)[3] reported Agate Beach, Oreg. mean surf temperatures and Wyatt and Gilbert (1971, 1972) reported monthly mean surface temperatures for various ports along the Oregon coast to be as much as several degrees lower during the later winter of 1971 than 1970.

[3]Gonor, J. J., and D. W. Elvin. 1971. Inshore sea surface temperature and salinity conditions at Agate Beach, and Yaquina Head, Oregon in 1971. Unpubl. data. School Oceanogr. Oreg. State Univ.

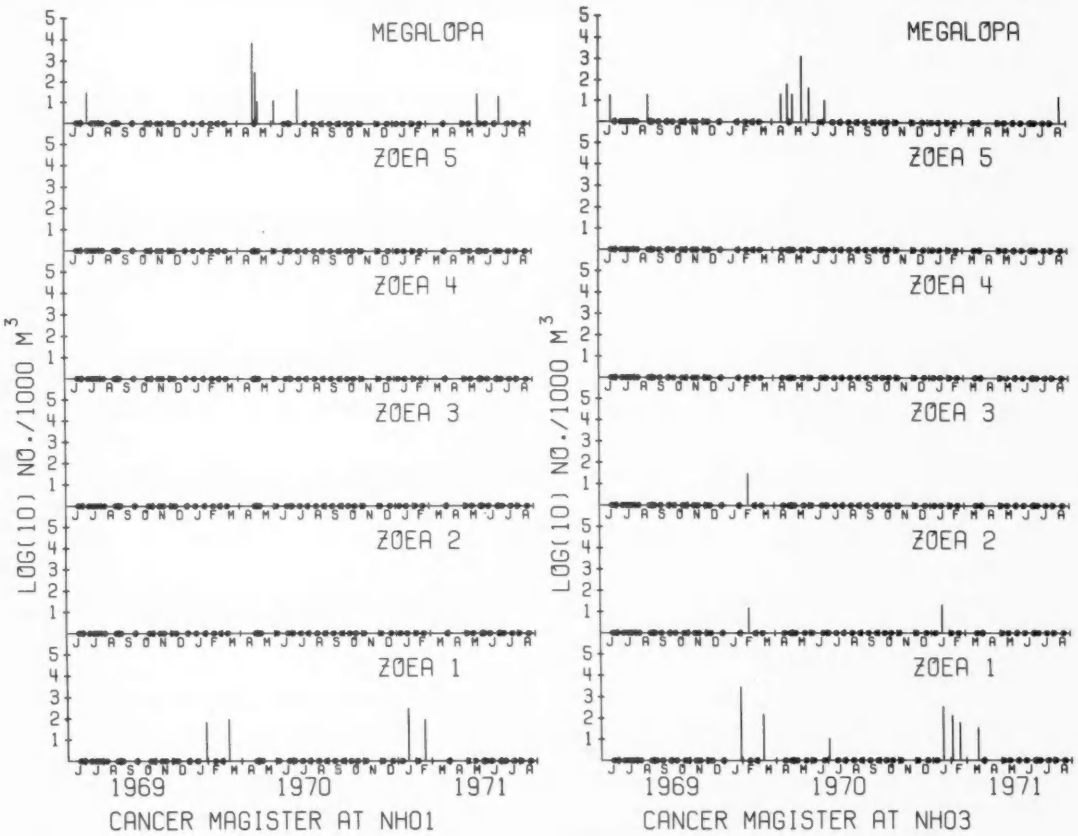
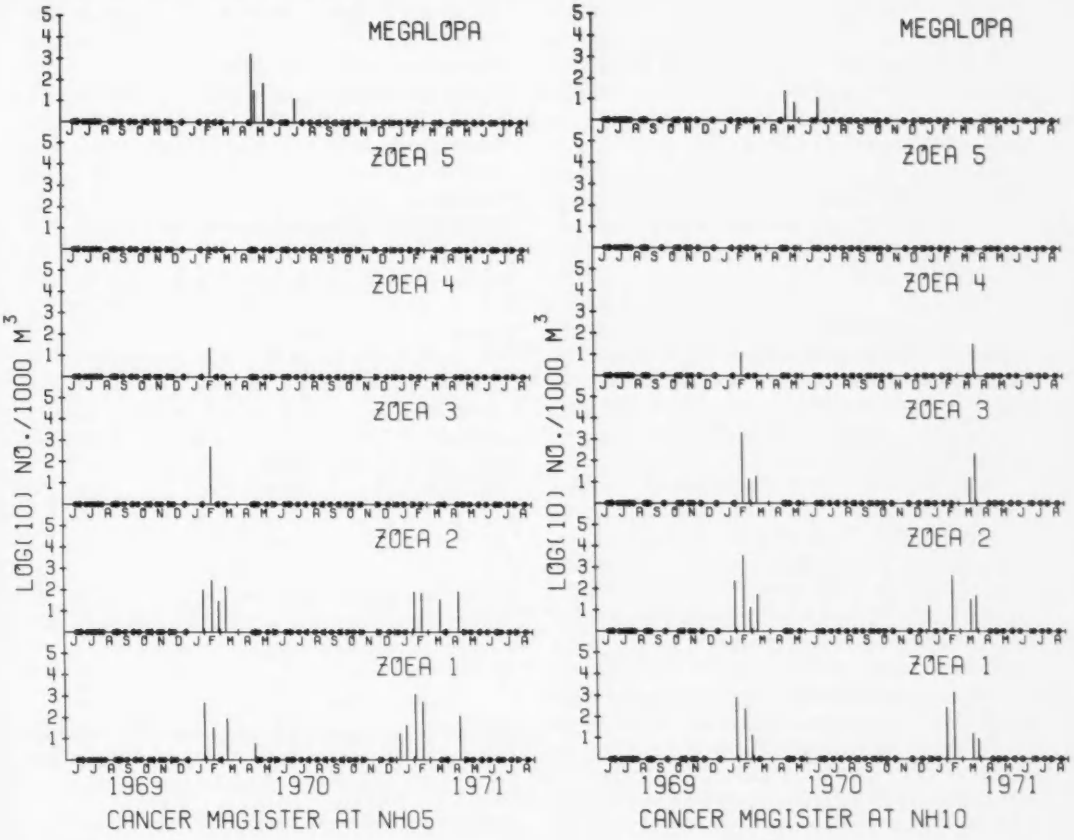


FIGURE 3.—Density of *Cancer magister* larvae at stations NH01, NH03, NH05, and NH10 from June 1969 through August 1971, collected with the 0.2-m bongo net sampler, 0.571-mm mesh.

Salinity values showed considerable variability among stations and months such that a generalized trend could not be observed between the two seasons. The anomalous winter of 1971 was further substantiated by Bakun's (1973) indices of coastal upwelling intensity for selected locations along the west coast of North America based on offshore Ekman surface wind transport from monthly mean surface atmospheric pressure data. Positive values indicate periods of coastal upwelling whereas negative values indicate downwelling. January and February of 1970 at lat. 45°N, long. 125°W show significantly greater negative indices (−98 and −71, respectively) than the same period in 1971 (−32 and −16, respectively). High negative values are indicative of strong downwelling along the coast which Bakun stated would accelerate the southward flow. In either case, more offshore surface water would be transported onshore. During the March transition period, the 1970 index was normal (+1); however during 1971 an anomalously high negative index (−49) occurred. This indicates that downwelling and subsequent transport of surface waters was more intense during March of 1971 than 1970. Downwelling also was more intense during March 1971 than in the previous 2 mo of that year. Drift bottle data compiled by Wyatt et al. (1971) reported a 14.7% return for bottles released off Newport from 25 February to 3 March 1970. By contrast, a 28.6% return occurred during 6-9 March 1971. The average percent return of drift bottles on all stations west of Newport, 1961-71, during both February and



March was 18% (Wyatt et al. 1972). High percentages of returns near 30% were observed only during February and March 1961, 1962, 1963, and 1967.

April 1970 showed a high positive index value (+25) indicative of upwelling processes, whereas downwelling was still in process during the same month in 1971 (−2). However, by May 1971 the upwelling intensity was twice the magnitude of that in 1970 (+66 and +33, respectively). In all regards the year 1971 can be considered the most anomalous whereas 1970 can be considered the least anomalous of the sampling period and the most typical over a 20-yr span. Kukla and Kukla (1974) reported large-scale global anomalies in weather patterns developing early in 1971. Snow cover in the northern hemisphere increased dramatically for the months of February, March, April, and September 1971.

Larval Population Analyses Between 1970 and 1971

Despite the rather restricted data set, a rigorous statistical analysis is attempted at this point to explore the relative importance of some environmental variables associated with the *C. magister* larval populations. An attempt is made to examine potential causative factors underlying the difference in larval abundance between 1970 and 1971 seasons. A basic assumption in the analysis is that the larval data collected in a single sampling transect are representative of a much larger homogeneous area. Patches of larvae may be quite localized so that differences in larval abundance from year to year may be due to dispersal and not mortality caused by an environmental variable per se. However, the distribution of adult breeding populations are

confined to shallow waters less than 50 m depth and appear fairly uniform along the Oregon coast based on commercial landings of legal-sized adults (Waldron 1958). This implies that the distribution of larvae along the entire Oregon nearshore area would be relatively homogeneous from year to year. Wind induced turbulence and mixing would tend to increase the homogeneity of the larval population despite any initial patchiness.

If we assume that the total number of *C. magister* larvae combined over the four inshore stations (NH01, NH03, NH05, NH10) is representative of the total population on a local basis, then the question may be asked whether there is a significant difference in the population means between the 2 yr, 1970 and 1971, and can a difference be explained using the concomitant observations of time, temperature, and salinity?

An analysis of multiple covariance was used to test this hypothesis on two sets of data for *C. magister* larvae. The first set of data compares the sampling period from 29 January 1970 to 29 July 1970 with that of 18 January 1971 to 21 July 1971. This period includes, for these 2 yr, the first major larval release through the time at which no megalopae were present in the water column. Larval density estimates from both sizes of mesh of the 0.2-m bongo net sampler were used in the analyses. Surface temperatures and salinities comprised the only complete data set for the two larval seasons and the average values of the four inshore stations were used for each sampling period. Nevertheless, sea surface temperatures and salinities are representative of nearshore subsurface conditions during the winter period from November through March-April as extensive wind mixing occurs in the shallow areas producing isothermal conditions (Renfro et al. 1971). During the spring and summer, a weak thermocline of less than 2°C exists in the nearshore area (<20 m). Larval and environmental data used in the analyses are given in Appendix Table 1.

The mathematical model used for the initial analysis was of the form:

$$Y = b + b_0(y) + b_1(t) + b_2(T) + b_3(S) + b_4(T^2) + b_5(S^2) + b_6(T \times S)$$

where, $Y = \log_{10}(X + 1)$ number of larvae per 4,000 m³ of water, b = a mean effect, y = a year effect, t = a time effect (days elapsed since 1 January), T = linear effect of sea surface temperature (°C), S = linear effect of sea surface salinity (‰), T^2 = quadratic effect of temperature, S^2 = quadratic effect of salinity, and $T \times S$ = interaction effect between temperature and salinity.

The b's in the model were estimated from a general linear hypothesis testing computer program contained in the Oregon State University Statistical Program Library. Various hypotheses can be specified by the user to test the importance of the individual parameters in the model.

A summary of the analysis on the initial run is given in Table 2. A highly significant difference (1% level) was found between y means after being adjusted for all the covariates in the model. However, only t was found to be highly significant in explaining the yearly difference. That is, the appearance of larvae in the plankton was of shorter duration in 1971 than in 1970. Subsequently, a new model was generated using only t as a covariate:

$$Y = b + b_0(y) + b_1(t).$$

The importance of t was again found to be highly significant in explaining the difference between y population means of *C. magister* larvae (Table 3).

TABLE 2. — A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January through July) by analysis of multiple covariance (full model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*-level
t	1	12.983	12.983	15.079**
T	1	1.323	1.323	1.537
S	1	0.120	0.120	0.140
T^2	1	0.513	0.513	0.594
S^2	1	0.296	0.296	0.344
$T \times S$	1	1.303	1.303	1.513
y (adjusted)	1	9.074	9.074	10.538**
Residual	44	37.887	0.861	

$^{**}F_{99(1,44)} = 7.12$

Fitted model: $Y = -11.313 + 0.470(y) - 0.018(t) - 5.076(T) + 2.576(S) + 0.043(T^2) - 0.060(S^2) + 0.127(T \times S)$.

		Mean of covariates					
Year	Mean Y	t	T	S	T^2	S^2	$T \times S$
1970	2.19518	124.21	10.36	32.23	109.05	1,040.49	333.13
1971	1.57263	109.38	10.01	31.71	102.74	1,007.00	316.70

TABLE 3. — A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January through July) by analysis of multiple covariance (reduced model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*-level
t	1	45.149	45.149	52.336**
y (adjusted)	1	9.448	9.448	11.218**
Residual	49	42.271	0.863	

$^{**}F_{99(1,49)} = 7.17$

Fitted model: $Y = 3.856 + 4.366(y) - 0.017(t)$.

The second data set compares the sampling period 29 January-2 May 1970 with 18 January-14 May 1971. The period selected compares the larval period prior to summer upwelling, eliminating the erratic surface temperature and salinity fluctuations. Most of the *C. magister* larvae are megalopae by early May.

The same full model was used in the initial run for the second data set and is presented in Table 4. There was a significant difference (5% level) between y means after being adjusted for all the covariates in the model. The covariates, t, T, and $T \times S$ were all significant.

TABLE 4. — A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January to May) by analysis of multiple covariance (full model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-level
t	1	6.807	6.807	7.073*
T	1	5.277	5.277	5.483*
S	1	0.156	0.156	0.162
T^2	1	0.018	0.018	0.019
S^2	1	0.012	0.012	0.012
$T \times S$	1	5.183	5.183	5.385*
y (adjusted)	1	6.260	6.260	6.504*
Residual	26	25.023	0.962	

*$F_{95(1,26)} = 4.22$

Fitted model: $Y = 180.944 + 0.712(y) - 0.024(t) - 20.294(T) - 4.907(S) - 0.037(T^2) - 0.022(S^2) + 0.656(T \times S)$.

		Mean of covariates					
Year	Mean Y	t	T	S	T^2	S^2	$T \times S$
1970	2.80494	90.56	10.35	31.76	107.91	1,010.36	328.08
1971	2.09844	80.13	9.59	31.28	92.82	979.08	299.81

The initial model was reduced to the following form:

$$Y = b + b_0(y) + b_1(t) + b^2(T) + b_3(S) + b_4(T \times S)$$

which greatly increased the significance of the parameters in the final model (Table 5). A highly significant difference (1% level) was found between y means after being adjusted for all the covariates. In explaining the difference between y means of *C. magister* larvae, the covariate t was most significant (1% level) followed by T and S, and $T \times S$ at the 5% level.

The foregoing analyses support the contention that there was a significant difference between the *C. magister* larval populations of 1970 and 1971. Fewer larvae appeared in 1971 and they appeared in the plankton for a shorter period of time suggesting widespread larval mortality. This apparent larval mortality was associated by these analyses with the colder surface temperatures and lower salinities that occurred during the winter of 1971. The direct effects of temperature and salinity on larval survival will be explored in the next section.

TABLE 5.—A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January to May) by analysis of multiple covariance (reduced model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-level
t	1	7.629	7.629	8.530**
T	1	5.859	5.859	6.551*
S	1	5.230	5.230	5.845*
$T \times S$	1	5.774	5.774	6.456*
y (adjusted)	1	8.650	8.650	9.672**
Residual	28	25.043	0.894	

*$F_{95(1,28)} = 4.20$; **$F_{99(1,28)} = 7.64$

Fitted model: $Y = 201.891 + 0.705(y) - 0.023(t) - 20.547(T) - 6.148(S) + 0.641(T \times S)$.

Temperature-Salinity Tolerance of Laboratory-Reared Larvae

A laboratory study by Reed (1969) determined the effects of temperature and salinity on the larval survival of *C. magister*. However, it was necessary to assess more thoroughly the effects of these factors on survival during development and to extrapolate from Reed's data in order to derive better estimates of larval survival at the low temperatures that occurred during the 1971 season. The response surface technique used in the analysis of his data is not only valuable in its predictive role, but also visually represents any change in response at various stages of development. Details of this response surface technique and its application to the study of marine ecology are discussed by Alderdice (1972).

A multiple regression analysis was applied to Reed's (1969) survival data of *C. magister* after 20, 30, 40, and 50 days of culture at experimental conditions. The mathematical model used in the analysis was of the form:

$$Y = b_0 + b_1(S) + b_2(T) + b_3(S^2) + b_4(T^2) + b_5(S \times T)$$

where, Y = percentage survival, b_0 = a constant, S = linear effect of salinity, T = linear effect of temperature, S^2 = quadratic effect of salinity, T^2 = quadratic effect of temperature, and $S \times T$ = interaction effect between salinity and temperature.

The b's in the model were estimated by a stepwise multiple regression computer program. Further details of the regression analysis are

given by Lough (1975a). The calculated regression coefficients from a particular equation are fitted by computer to a full quadratic equation in temperature and salinity in order to print a contour diagram of the response surface. Temperature and salinity scales on all plots were set to range beyond the experimental conditions in order to facilitate response comparison and to allow the overall form of the surface to be visualized. Contours extrapolated beyond the experimental data lie outside the dotted lines.

A summary of the multiple regression analyses on survival after the various periods of rearing and the response surfaces are given in Table 6 and Figure 4. The analyses indicated that after 20 days of rearing under the experimental conditions S and S^2 were the two most important variables in the model. T and $S \times T$ were of lesser importance but still contributed significantly to the model. Analyses of the later rearing periods of *C. magister* emphasized the effect of temperature and showed the decreasing importance of both S and S^2 and $S \times T$. This trend is more evident when one compares the response surface plots from 20 through 50 days of rearing. After 20 days of rearing, the response surface contours are nearly circular, with a slight tilt to the main axis, indicating a small interaction effect. The axis of the contours tilts progressively towards the temperature axis until, at 50 days of rearing, the contour axis is almost perpendicular to the temperature axis. Also, the survival contours progressively constrict about the temperature axis with time showing the narrowing of the temperature range tolerated by the larvae. Maximum survival (80% contour) at 20 days is predicted to occur between 6.5° and 17.5°C and 21.5 and 35.0‰, while at 50 days, maximum survival is predicted to occur between 9.0° and 15.0°C and above 28.5‰. The area of maximum survival (80% contour) shifts somewhat during the 20- to 50-day period from an initial low salinity-wide temperature range to a high salinity-low temperature tolerance. However, when the 20- and 50-day survival polynomials were tested by an analysis of covariance (Ostle 1963:205), they were not found significantly different in their response (Table 7). In summary, salinity appears to exert an immediate effect on *C. magister* larval survival, while the effect of temperature becomes increasingly important with time.

Survival at a given temperature, salinity, and time can now be estimated using the fitted equations. All of the fitted equations for the four time

TABLE 6. — Multiple regression analyses of *Cancer magister* larval survival in 20 temperature and salinity combinations.

Regression step number	Variable	R^2	F-value	Degrees of freedom	Significance level	Coefficients	t-value	Significance level
				20 days				
1	S	0.505	18.378	(1,18)	1%	29.4369	4.069	1%
2	S^2	0.591	3.723	(2,17)	5%	−0.4720	3.040	1%
3	T^2	0.659	3.030	(3,16)	N.S.	−0.7068	4.635	1%
4	T	0.834	15.819	(4,15)	1%	23.4636	4.559	1%
5	$S \times T$	0.865	3.272	(5,14)	5%	−0.2277	1.809	N.S.[1]
	Constant					−457.6092		
				30 days				
1	S	0.417	12.878	(1,18)	1%	18.3726	2.026	N.S.
2	T^2	0.529	4.044	(2,17)	5%	−0.6903	3.611	1%
3	T	0.702	9.290	(3,16)	1%	23.0272	3.569	1%
4	$S \times T$	0.744	2.443	(4,15)	N.S.	−0.2503	1.586	N.S.
5	S^2	0.768	1.446	(5,14)	N.S.	−0.2340	1.202	N.S.
	Constant					−335.2867		
				40 days				
1	S	0.416	12.830	(1,18)	1%	14.3243	1.602	N.S.
2	T^2	0.491	2.511	(2,17)	N.S.	−0.8113	4.305	1%
3	T	0.744	15.824	(3,16)	1%	25.5095	4.011	1%
4	$S \times T$	0.768	1.509	(4,15)	N.S.	−0.1892	1.217	N.S.
5	S^2	0.779	0.713	(5,14)	N.S.	−0.1620	0.844	N.S.
	Constant					−313.8493		
				50 days				
1	S	0.373	10.717	(1,18)	1%	13.4195	1.687	N.S.
2	T^2	0.432	1.756	(2,17)	N.S.	−0.8265	4.931	1%
3	T	0.757	21.339	(3,16)	1%	25.7928	4.559	1%
4	$S \times T$	0.778	1.451	(4,15)	N.S.	−0.1662	1.201	N.S.
5	S^2	0.791	0.901	(5,14)	N.S.	−0.1620	0.949	N.S.
	Constant					−305.2337		

[1]N.S. = Not significant.

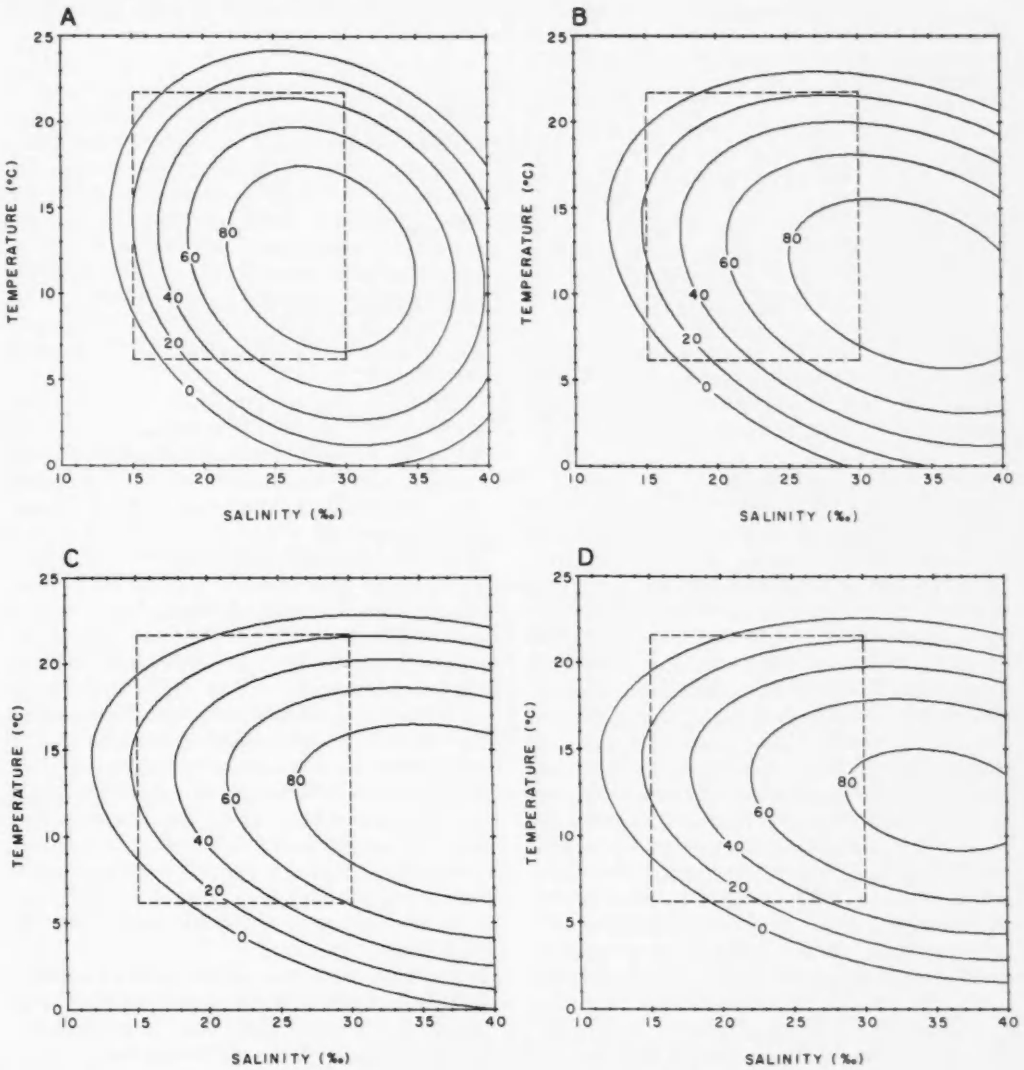


FIGURE 4. — Response surface estimation of percent survival of *Cancer magister* larvae after (A) 20 days, (B) 30 days, (C) 40 days, and (D) 50 days of development at 20 different temperature and salinity combinations.

periods explained a significant 77-87% of the variance in the data. The lowest surface temperature and salinity reported for any sampled station during the 1971 season was 7.4°C and 25.17‰. After 20 days at this combination, 76.8% survival is predicted; after 50 days, 44.6% survival. The monthly mean surface temperature and salinity compiled at the Oregon State University Marine Science Center dock, Newport, is reported by Wyatt and Gilbert (1972) for March 1971 to be 8.81°C and 30.12‰. Survival of 92.3% is predicted at this temperature and salinity combination after 20 days, and 71.0% survival after 50 days. The direct effect of these temperatures and salinities found off the central Oregon coast on the survival of *C. magister* larvae would appear to

TABLE 7. — An analysis of covariance between the 20- and 50-day survival polynomials of *Cancer magister* larvae. Null hypothesis: no significant difference between 20- and 50-day survival polynomials.

Source of variation	df	Sum of squares	Mean square	*F*-value
Polynomial 1: 20-day survival	14	4,217.780		
Polynomial 2: 50-day survival	14	5,096.684		
Total: Polynomial 1 and 2	28	9,314.464	332.659	
Polynomial 3: Combined 20- and 50-day survival	34	13,287.052		
Difference: Polynomial 3 and total	6	3,972.588	662.098	[1]1.99

[1]Not significant, $F_{95(6,25)} = 2.44$.

be minimal. Forty-five percent survival would still occur, even after an unrealistic period of 50 days at nonconservative temperatures and salinities.

Gut-Fullness Analysis of Planktonic Larvae

The physical appearance of *C. magister* larvae was examined for clues to the difference in the larval populations between the two seasons, 1970 and 1971. Whatever happened to the larvae occurred early in their development during the months of February and March 1971, as a marked decrease in the total larval population was observed by the second zoeal stage. Those larvae examined from the 1971 season appeared more flaccid with a soft exoskeleton, had less eye pigmentation, and were more transparent compared to the larvae caught during the 1970 season. However, these features of appearance could not be readily quantified. Further examination indicated a possible difference on a population basis in the amount of food in their guts among stages, stations, and years. Differences in larval gut-fullness may indicate good versus poor food availability, or possibly a dying larval population weakened by some factor in their environment other than food.

Food and/or feces in the guts could readily be seen through the body wall up to the fourth or fifth zoeal stage and a close estimation of the percentage fullness could be made by noting the proportion of gut segments filled with food. The larval body can be divided into eight equal segments; the thorax constituting twice the length of an abdominal segment. The food or feces was considered to be of the same approximate diameter and could be estimated to within 3% of the total gut length. A sample size of 30 larvae was necessary before any significant difference could be considered.

The 0.2-m bongo net samples were used to compare the 1970 and 1971 larval seasons at stations NH01, NH03, NH05, and NH10. Samples were combined with both meshes of the 0.2-m bongo nets. Only whole larvae were used and usually the entire sample was analyzed. Specimens from the 0.7-m bongo net samples were used to compare inshore-offshore larval gut-fullness between the 12 stations, NH01 through NH60, for the 1971 season.

Zoea 1 larvae from the 1970 season showed maximum mean percentage gut-fullness at stations NH03 and NH10 compared to those from NH01 and NH05 (Table 8). A general decrease in gut-fullness was observed with increasing stage of development. Surprisingly, all zoeal stages of larvae caught during the 1971 season showed an increase in gut-fullness over those of the 1970 season. The notable exception occurred for zoea 1 larvae at station NH03, where the 1971 gut-fullness is significantly lower than that for the 1970 season.

The onshore-offshore comparison showed that the greatest gut-fullness for any larval stage oc-

TABLE 8. — A comparison of *Cancer magister* larval gut-fullness[1] between 1970 and 1971 at four Newport Hydrographic line (NH) stations.[2]

Stage	Year	NH01	NH03	NH05	NH10
Zoea 1	1970	13.19 ± 2.74(4)	31.23** ± 0.06(126)	19.64 ± 0.12(65)	29.53 ± 0.07(106)
	1971	14.26 ± 0.34(19)	9.86 ± 0.10(78)	24.10** ± 0.03(241)	36.13** ± 0.04(187)
Zoea 2	1970		7.56 ± 1.97(5)	15.57 ± 0.10(72)	12.94 ± 0.02(269)
	1971		25.00 ± (1)	23.29** ± 0.24(38)	30.39** ± 0.11(87)
Zoea 3	1970		10.49 ± 10.49(2)	23.76 ± 0.09(81)	14.02 ± 0.02(212)
	1971			18.75 ± (1)	20.20** ± 0.09(51)
Zoea 4	1970			9.40 ± 3.36(4)	15.99 ± 1.19(6)
	1971				19.50 ± 1.61(7)
Zoea 5	1970				
	1971				

[1]Gut-fullness is expressed as a reconverted arcsin$\sqrt{\text{percentage}}$ transformed mean followed by its standard error and the number of observations in parentheses.
[2]The station samples in this table represent the combined specimens from both mesh sizes of the 0.2-m bongo net sampler.
**1% level significant difference between yearly means based on a two-sample *t*-test.

TABLE 9. — A comparison of *Cancer magister* larval gut-fullness[1] between 12 Newport Hydrographic line (NH) stations for 1971.[2]

Station	Zoea 1	Zoea 2	Zoea 3	Zoea 4	Zoea 5
NH01	8.51* ± 1.33(9)				
NH03	10.51** ± 0.06(82)	0.79 ± 0.79(2)	0.0 ± (1)		
NH05	27.89** ± 0.05(134)	17.57** ± 1.09(14)			
NH10	26.51** ± 0.07(137)	29.79** ± 0.07(109)	45.77* ± 0.71(12)		
NH15	23.50** ± 0.07(76)	35.11** ± 0.33(36)	60.77** ± 2.27(8)		
NH20	34.43** ± 0.12(72)	23.69** ± 0.13(69)	20.99 ± 0.12(5)	25.00 ± (1)	43.75 ± (1)
NH25	6.26** ± 0.25(33)	6.41 ± 0.48(20)	3.01 ± 3.01(3)		
NH30	11.51 ± 0.07(56)	7.75 ± 0.39(9)	23.41 ± 0.52(4)		25.00 ± (1)
NH35		12.03 ± 0.99(3)	17.09 ± 0.16(5)	18.75 ± (1)	
NH40	53.14 ± 0.10(2)	0.0 ± (1)	6.70 ± 6.70(2)	6.25 ± (1)	13.92 ± 5.06(3)
NH50		6.25 ± (1)	0.0 ± 0.0 (2)	19.39 ± 19.39(2)	3.02 ± 1.74(8)
NH60	0.71 ± 0.71(3)	0.13 ± 0.13(10)	0.0 ± 0.0 (4)	0.0 ± 0.0(15)	0.0 ± 0.0 (3)

[1]Gut-fullness is expressed as a reconverted arcsin$\sqrt{\text{percentage}}$ transformed mean followed by its standard error and the number of observations in parentheses.

[2]The station samples in this table are from the 0.7-m bongo net sampler exclusively.

*5% level significant difference between successive station means based on two-sample *t*-tests.

**1% level significant difference between successive station means based on two-sample *t*-tests.

curred between stations NH05 and NH20 (Table 9). Any zoeal stage caught within NH03 and farther offshore than NH20 showed a marked decrease in gut-fullness.

DISCUSSION

The initial appearance of *C. magister* larvae in the plankton off the central Oregon coast in late January and early February occurs at a time when sea surface temperatures are generally warming after the yearly mean low in January (Gonor et al. 1970). High densities of early stage zoea caught within 3-10 miles of shore are in agreement with the known distribution of the adults at this time. Relatively few occurrences of early stage larvae were found beyond 10 miles of shore during the sampling period as the northward flowing Davidson Current tends to retain the early developing larvae in the nearshore area. A very strong onshore component of the current has been observed within 5 miles of shore (Keene 1971; Wyatt et al. 1972; Holton and Elliot 1973). During the March and April transition period when the northward Davidson Current is replaced by currents flowing to the south and southwest, the larvae have developed to late stage zoea and megalopae. The bulk of the *C. magister* megalopae settle out of the water and metamorphose to juveniles by April and May before the onset of intense coastal upwelling in June and July, thus reducing the chance of being carried offshore by the resulting Ekman Current. During all seasons along the coast, larvae which occur increasingly closer to shore would be subject to decreasing current transport either alongshore or offshore.

1970 Season

It was observed during the 1970 larval season of *C. magister* that the late zoeal stages "disappeared" or were greatly reduced in numbers in the inshore sampling area, whereupon the megalopae reappeared after the proper time interval in densities comparable to those of the previously sampled zoea. Hypotheses to explain their disappearance and reappearance are as follows: 1) the late zoea were misidentified, 2) some stages are skipped in development, 3) the sampling interval missed those stages, 4) avoidance of the samplers increases with zoeal stages of development but decreases at megalopal stage, 5) the late zoeal larvae are carried offshore or alongshore but upon molting to the megalopal stages are transported onshore or back to their original release point, 6) the larvae were very dispersed at late zoeal development so that the volume of water filtered was not adequate, or 7) late stage zoea are resting on the bottom or below the depth sampled.

The late stages of *C. magister* larvae were not misidentified as they are morphologically distinct by this time and are nearly twice the size of any other local cancrid species. Apparently, the late larval stages of *C. magister* were not skipped in their development since zoea 4 and 5 stages were collected on the offshore stations in late March and early April. It is not believed that the late zoeal stages have greater swimming ability compared to the early zoea and megalopa which would permit them to avoid the samplers to a greater degree. On the contrary, personal observations of the late stage larvae in laboratory culture show them to be sluggish swimmers that

spend considerable time resting on the bottom of the rearing vessel.

A species such as *C. magister*, which has a larval life of approximately 130 days, could conceivably be transported northward about 600 miles along the North Pacific coast as Wyatt et al. (1972) reported that the winter surface currents based on drift bottle studies have a mean speed of 0.2 knots, or a drift of 150 miles per month. The Ekman transport of surface waters due to wind stress decreases exponentially with depth due to frictional resistance, so that when the current has fallen to about one-twenty third that of the surface, this subsurface flow is negligible or reverse to that of the surface currents (Sverdrup et al. 1942). Recent studies indicate wind driven water motion extends to a depth of about 10 m (Bourke et al. 1971). If the larval population resides about 5m below the surface where the wind induced current is about one-quarter that of the surface, then the larvae would only be transported 150 miles in a linear distance. Larvae located in the water column below 5m depth, particularly the later zoeal stages, would experience relatively little transport in any direction. Holton and Elliot (1973) reported the greatest abundance and density of zooplankton containing crab larvae occurred at about 15m depth at nearshore stations off Newport during the daylight hours. Hypothetically, larvae released in January-February could be transported north along the coast in the surface currents and, after the transition period of currents in March, travel south a comparable distance in April and May. Or, taking into consideration the fact that the older stages may reside deeper into the water column, they could conceivably travel north in the surface currents as early zoea and travel south again as late larvae in a weak underlying countercurrent, but this seems unlikely. Huyer et al. (1975) reported the northward currents along the central Oregon coast essentially are constant with depth during the winter and southward at all depths in the spring but stronger at the surface. Larvae occurring within 3-5 miles of the coast probably are caught within a system of eddies and countercurrents characteristic of this zone, retarding large-scale dispersal in any direction. The mechanistic concepts of recruitment seem too contrived and unnecessary if stochastic processes are the general rule for species producing large numbers of expendable young. Most investigators would agree that the great majority of the pelagic larvae of marine invertebrates are lost to the population and that only a very small percentage of annual recruits are normally required to maintain a stable population for longer-lived adults. *Cancer magister* lives 4 or 5 yr so that a population unexploited by man would only require recruitment every other year or so. The fact that the adult populations are not retreating northward supports the view that at least some of the larvae are retained in the same general area as their point of origin.

The low densities of late stage larvae collected in the offshore area indicated that the small volume of water filtered on the inshore stations could account for their disappearance or reduced numbers.

Knowledge of their vertical location within the water column at different stages of development is important in understanding their spatial distribution and local abundance. However, a separate study of the larvae within the upper 150 m was not undertaken. Most crab larvae are photopositive to light in their early stages and migrate to the surface layers, whereas the late stages respond photonegatively and are found in the deeper layers near the bottom as they prepare to molt to juveniles (Thorson 1964). The larvae of *C. magister* appear to follow this same general pattern except that the early megalopal stage shows anomalous behavior as they have been observed to "swarm" near the sea surface along the coast (Cleaver 1949; Gaumer 1971; pers. obs.). Personal laboratory observations, as well as those by MacKay (1942) and others, substantiate the fact that the early zoea and megalopa of *C. magister* are generally photopositive in contrast to the late zoeal stages which are neutral or photonegative.

A scheme is proposed which would explain their distribution and abundance within 10 miles of the coast taking into account the differential behavioral response to light of the various larval stages. Newly hatched zoeal larvae are strongly photopositive and swim to the surface where current transport during the winter is generally onshore. They become progressively heavier and less photopositive with development until in the late zoeal stages they are neutral or responding negatively to light. As a consequence, the late zoeal stages reside in the deeper layers of water, possibly within a few meters of the bottom. They are now maximally dispersed in the nearshore area. Upon molting to the megalopic stage they are temporarily strongly photopositive to light and coupled with their increased powers of

locomotion, they swarm to the surface again and are congregated by the prevailing currents usually in a band within 5 miles of the coast. If the late zoeal larvae do in fact reside near the sea bottom, the onshore drift current within 10-20 m of the bottom would prevent them from being transported offshore. Bottom flow in waters less than 40 m deep is towards the coast in the direction of wave travel throughout the year (Gross et al. 1969). The behavior of the larvae within the water column in relation to the hydrological features of the nearshore area under usual circumstances tends to restrict dispersal of the larvae to any great degree.

1971 Season

The sparseness of *C. magister* late zoeal larvae and megalopae during the 1971 season implies that a mass mortality occurred in the early zoeal stages. This apparent mortality was associated with sea surface temperature and salinity in analyses of covariance, but larval survival predicted through response surface methodology and gut-fullness analysis did not substantially explain their sparseness. The lack of highly supportive evidence leads to further speculation as to the causes of larval mortality in the plankton.

Hypothesis 1: Direct Effects of Temperature and Salinity

Sea surface temperature, and salinity to a lesser degree, were important environmental factors in explaining the difference in yearly larval population means of *C. magister* by analyses of multiple covariance. However, the statistical importance of these factors in determining larval abundance may be misleading. A wide temperature gradient during a larval season, i.e., a steep slope, could be statistically significant, but the range of temperatures may be well within the tolerance limits of an organism. In contrast, the salinity gradient during the same larval season is usually narrow resulting in a statistically nonsignificant slope, which may still occur outside the range tolerated by the larvae. Also, the erratic surface temperature and salinity fluctuations that occurred during the summer upwelling may cancel the effect of a significant gradient that occurred earlier in winter and spring.

Cancer magister larvae were reared by Reed (1969) under various temperature-salinity combinations and he concluded that these factors, as they normally occur off the Oregon coast, would not significantly affect survival. Response surface techniques, using Reed's data, predicted about 45% survival under the extreme temperatures and salinities that occurred during February and March 1971. The sea surface temperatures and salinities used in the analysis probably represent the most extreme long-term conditions that the larvae could have experienced in the field. Larvae several meters below the surface may be protected from the more extreme fluctuations of temperature and salinity, but some degree of exposure seems certain in view of the fact that extensive wind mixing occurs in shallow waters along the coast. The North Pacific is characterized by heavy precipitation during the fall and winter seasons resulting in considerable land drainage and river runoff along the nearshore area. Larvae along the coast, particularly near the mouths of bays and rivers, may lie in the low-salinity plume waters before sufficient mixing occurs. Harder (1968) reported that many planktonic organisms tend to accumulate near density interfaces that frequently occur in natural waters. Some species of copepods were observed under laboratory conditions to react to extremely small changes in density. Whether *C. magister* larvae have the ability to avoid these low-salinity surface waters that may be detrimental to them is not known. The early zoeal larvae would seem most vulnerable to low surface salinity as their behavioral response directs them to the surface and their swimming ability is slight compared to the megalops stage. Early larval ability to avoid low-salinity surface waters would have to be sufficient to overcome the increased storm-induced mixing during this season. The mortality rate of *C. magister* larvae reared in the laboratory under optimum conditions was constant and minimal throughout development (Reed 1969). Mortality increased greatly for larvae reared at 20‰ salinity; early zoeal larvae were killed within a short period in salinities less than 20‰. In addition, both the lower range of salinities and temperatures used in his experiments increased the duration of the larval instars where survival could be monitored for a sufficient time period.

It is difficult to evaluate the extent to which results from laboratory studies approach reality in order to understand how environmental variables may affect survival. Larvae reared at sub-

optimal conditions have been observed to survive for considerable periods of time, apparently unable to molt successfully. These same larvae eventually die, but laboratory experiments often are terminated before full mortality can be observed. Low salinity during the winter of 1971 may have been an important factor resulting in the demise of *C. magister* larvae that year. Subtle changes in the flux and composition of the internal ionic constituents can alter the molting process; larvae which appear normal in early development may mask deficiencies that express themselves later in development. Nevertheless, short-term exposure to extreme conditions may be just as detrimental as slightly suboptimal conditions over a long period of time (cf. Lough and Gonor 1973a, b). Although the nearshore surf salinities on a monthly average are in the range of tolerance by the larvae, daily measurements occasionally drop below 20‰ (Gonor et al. 1970). No larvae survived below 20‰ salinity in Reed's (1969) laboratory study.

The effect of low salinity in conjunction with wider than normal temperatures may play an important role in larval survival as indicated from the analyses. Low and high temperatures greatly accentuated the effects of marginally dilute salinities on *C. magister* larval survival. But again, the ecological significance of a synergistic effect has not been fully established in this study. More detailed, short-term studies of salinity-temperature variability and larval monitoring are needed in the nearshore area. Sastry and McCarthy (1973) observed distinct differences in temperature-salinity tolerances and metabolic responses of the larvae of two species of *Cancer* sympatrically distributed along the east coast of North America. Complete development for *C. irroratus* larvae occurred over a wide range of temperatures, whereas *C. borealis* larvae was restricted to a narrow range. The metabolic-temperature pattern of *C. irroratus* larvae indicated a progessive narrowing in temperature sensitivity. In contrast, the early stages of *C. borealis* initially were sensitive to warmer temperatures but in the later stages sensitivity shifted to colder temperatures. Hatching of the two *Cancer* species is separated in time so that the diverse metabolic responses observed are believed to be adaptations by larvae of the two species to the different temperature conditions encountered.

The combined effects of salinity and temperature have been studied under controlled laboratory conditions on other species of brachyuran larvae by Costlow et al. (1960, 1962, 1966), Costlow and Bookhout (1962), and Costlow (1967). Although the adults inhabit euryhaline waters, specific larval stages have been shown to require restricted ranges of salinity and temperature to varying degrees for complete development. In many cases, both temperature and salinity and the interaction of various combinations of the two environmental variables were observed to affect larval survival and retard development. Salinity generally has an immediate effect on survival while temperature appears to play a modifying role within the extremes of tolerance. Most of their work indicates that mortality was highest during the early zoeal stages and that the megalops stage was the least subject to environmental stress, although exceptions are reported. Recently, Costlow and Bookhout (1971) investigated the effects of cyclic temperatures compared to constant temperatures on the larvae of the estuarine mud crab, *Rhithropanopeus harrisii*. Duration of larval life and survival were about the same but survival was enhanced under cyclic temperatures at the higher end of the experimental range. Short-term fluctuations in temperature or other environmental variables throughout the water column have not been adequately monitored along the North Pacific coast. Their effect on *C. magister* larvae is not known and should be investigated.

Hypothesis 2: Food Quality and Quantity

May (1974) reviewed Hjort's (1914) critical period concept for fish larvae since Marr's (1956) evaluation and concluded from recent work that starvation may be an important cause of mortality, especially during the period immediately following the yolk sac stage. Although crab larvae do not have a strictly comparable yolk sac stage in their planktonic life, adequate food densities for efficient feeding may be of critical importance during a brief period following hatching. There is limited knowledge concerning the types of food organisms normally available and selected by *C. magister* larvae and concerning the densities of these food organisms sufficient for development. Most crab larvae are omnivorous, requiring substantial protein in their diet (Costlow and Sastry 1966; and others). Attempts to distinguish gut contents of field-caught *C. magister* larvae were unsuccessful in the present study. However, the

specific kind of food organism encountered may not be as important as its size. The size of food organisms available for each larval stage must be within a restricted range in order for a larva to successfully capture and ingest. The progression of larval size with development would indicate that the different larval stages can utilize increasingly greater sizes of food organisms. Reed (1969) found in laboratory culture that the larvae of *C. magister* survived well feeding on *Artemia salina* (0.475-0.752 mm length) and *Balanus gladula* nauplii (0.370-0.420 mm length), but would only survive for a limited period on smaller size veliger larvae of *Mytilus edulis* (0.100-0.300 mm length?). He also reported that unfed *C. magister* zoea larvae would only survive for 14 days. This implies that under natural conditions larvae will not survive if a suitable food organism is delayed in its appearance by more than 2 wk, and that certain kinds of food organisms selected by the larvae are nutritionally inadequate for their long-term metabolic needs.

Chamberlain (1961, 1962) reared the larvae of two xanthid crabs, *Neopanope texana sayi* and *Rhithropanopeus harrisii*, on a variety of foods and found that development was retarded when larvae were fed on a mixture of nauplii and algae. Larvae fed algae alone would not molt and only lived 6-10 days in culture. Algae appeared to be nutritionally inadequate for successful development and restricts the intake of more suitable food by indiscriminate larval feeding. Costlow and Sastry (1966) suggested that high mortality of *Callinectes sapidus* larvae at the time of the third zoeal stage in nutritionally inadequate culture may be due to the initial availability of a large pool of free amino acids within the eggs through the first and second zoeal stages. They also pointed out that the variability in tolerance to suboptimal conditions may be related to the size of such a free amino acid pool.

Although the gut-fullness analysis in the present study did not provide insight into the difference in larval abundance between the 2 yr, it did suggest the existence of an optimum zone for adequate feeding between 3 and 20 miles offshore where suitable kinds and densities of food organisms occur. Zooplankton volumes along the Washington coast decrease to a minimum level during the winter and increase to maximum levels during the spring (Frolander 1962). During the winter, the volume of zooplankton and abundance of copepods were greater inshore than offshore as a consequence of the onshore transport of surface waters (Frolander 1962; Anderson 1964; Peterson 1972). Anomalous weather conditions such as occurred during the winter of 1971 may have been ultimately responsible for alterations in the usual types and availability of food organisms encountered during the first few weeks of larval feeding.

Hypothesis 3: Predators and Competitors

The importance of the combined or separate effects of predation and competition on larval populations is difficult to assess. Predation has generally been regarded as the major cause of larval mortality (Thorson 1946, 1950). Lebour (1919a, b, 1920, 1921, 1922, 1923) observed many species of young fish and medusae to prey upon crab larvae as well as most other small organisms in the plankton. Cannibalism is well known in laboratory culture. Knudsen (1960) observed in the laboratory that xanthid first stage zoea were eaten by older zoea and megalops as well as by copepods. Other predators known to feed on marine larvae, such as ctenophores, chaetognaths, euphausiids, and shrimps, appear seasonally in high densities along the North Pacific coast. Their effect on larval populations has not been fully ascertained. Peterson (1972) compared the ratios of copepod nauplii to total copepods off the Washington coast and found that more nauplii were hatched inshore than offshore throughout the year, but fewer developed to adults suggesting greater predation in the inshore area. Predation was reduced during the winter compared to other seasons within the inshore area. These findings might similarly apply to relative predation rates on *C. magister* larvae along the North Pacific coast.

Factors in the environment such as abnormally cold temperatures or lack of food that extend the pelagic life of the larval phase have been considered detrimental due to predation. It has been assumed that the longer the larvae remain in the plankton the more they will be preyed upon, although predation pressure upon their recruitment to the benthic habitat may be just as great, or greater (Thorson 1966). Larvae genetically feeble or weakened by some environmental factors may be more subject to predation so that under usual circumstances, the importance of predation may be secondary in mortality processes. The effect of predation on larval populations

would not seem to be constant in the heterogeneous marine environment, but would more likely vary in intensity both temporally and spatially. Predation may only be a dominant factor in unusual years and/or on a small-scale basis.

Other members of the plankton community undoubtedly feed on the same food organisms as *C. magister* and competition may become an important factor when these food organisms become sparse. One potential competitor was tentatively identified as *C. oregonensis*. Its larvae are very abundant in the inshore area and cooccur with those of *C. magister*. Both species are morphologically similar and pass through the same number of larval stages, except that the larvae of *C. magister* become increasingly larger with development. There are studies showing the antagonistic effects of a mutually shared food resource. Brooks and Dodson (1965), in a study of two species of freshwater *Daphnia*, concluded that the larger species was more efficient in collecting both small and large particles and would competitively exclude the smaller species as long as size dependent predation was of low intensity. Conversely, Schoener (1969), in a theoretical study, concluded that large predators ate an equal or a greater range of food compared to the smaller ones as long as food was at some upper level. But, as food abundance was reduced, the optimal predator size shifted towards the smaller predator. Similar situations could conceivably occur and explain why *C. magister* larvae were less numerous in 1971. The interactions of hierarchies of predators and their prey involving temporal and spatial changes in densities and size frequencies can be exceedingly complex.

Hypothesis 4: Oceanic currents and multiple environmental effects

Planktonic organisms have limited means of locomotion and consequently are subject to the vagaries of oceanic currents. Changes in the strength or timing of these currents can be ultimately responsible for the success or failure of larval populations and their adult stocks (Coe 1956). The transport of entire larval stocks out of their normal environment can have catastrophic results for annual recruitment.

During the winter-spring larval period of *C. magister*, the major nearshore oceanographic feature is the northerly intrusion of the Davidson Current along the Oregon-Washington coast and its reversal in March-April. The strength and duration of the Davidson Current are critical factors in the initiation, development, and persistence of seasonally dominant plankton communities. Southern neritic zooplankton species appear abundant off the Oregon and Washington coasts during fall and winter and are believed to be carried by the northerly surface drift (Cross and Small 1967; Miller 1972; Frolander et al. 1973). Frolander (1962) observed widespread anomalous conditions off the Washington coast during February 1958, compared to the previous year. Lower plankton volumes and a change in plankton species were associated with an increase in the surface temperatures, a decrease in dissolved inorganic phosphate, and unusual weather during the anomalous February. These events were believed to be the result of southerly offshore waters moving into the coastal area to a larger extent that year.

Superimposed upon the nearshore currents with their characteristic water properties, a dominant modifying process results from precipitation and river runoff. A band of low salinity occurs all along the North Pacific coast. Little information is available on the effect of the heavy river runoff on the endemic plankton populations in the neritic zone, but some studies have been done concerning the effect of the Columbia River plume on the physical processes and biota over its range of influence (Anderson 1972). The Columbia River effluent flows north along the coast of Washington during the winter in response to the prevailing southwesterly winds (Barnes et al. 1972). Hobson (1966) and Anderson (1972) observed that chlorophyll and productivity at the surface of the plume and ambient waters were higher than nearby oceanic waters due to the increased stability of the water column providing an environment where phytoplankton could accumulate. The major influence of the Columbia River plume on phytoplankton development is believed to be in the timing of events. Phytoplankton populations can develop 3-5 wk earlier in the plume due to the increased stabilization. Heinrich (1962, 1968) stated that the seasonal cycle of phytoplankton communities are less balanced in the neritic zone and that the phytoplankton populations in this area can vary depending on the timing and differential growth of relative copepod species. Shifts in weather patterns create corresponding changes in nearshore currents resulting in the intrusion and displacement of endemic

planktons. Nearshore modifying processes can change the character of these communities setting forth new interactions among the populations.

Anomalous hydrographic and meteorological conditions were observed along the Oregon coast during the winter of 1971 in the present study. Its effect on the plankton populations to date only have been investigated in relation to *C. magister* larvae. To what extent did the relaxation of onshore transport of surface waters during January and February with subsequent increased transport in March 1971, compared to the same period in 1970, affect the dynamics of the *C. magister* larval population? The circumstantial evidence suggests that heavy mortality of the larvae occurred in 1971. However, the difference in larval abundance for the 2 yr may not be real if the larvae were quite localized in their alongshore distribution and moved out of the study area. Sampling was not conducted in other areas for those years to fully answer this point. In addition, the late zoeal stages were undersampled both years leaving a gap in our knowledge of their true numbers, distribution, and condition. Assuming that a mass mortality of larvae did, in fact, occur in the study area, what are the most likely environmental mechanisms? Did the decreased onshore surface water transport in early winter of 1971 relative to 1970 allow more larvae to be carried offshore that year where food abundance was lower, etc.? Any larvae swept off the shelf area that survived would still probably be beyond successful recruitment to the adult nearshore population. Did the greater onshore transport of surface waters during late winter of 1971 move the bulk of the larval population closer to shore into a suboptimal environment too early in their development? What is the effect of the increased precipitation and river runoff during the winter of 1971 that reduced nearshore salinities? Was a phytoplankton bloom initiated earlier in the season and how did it affect populations of other planktonic organisms utilized as food for *C. magister* larvae? Chamberlain (1961) commented that, for crab larvae feeding indiscriminately on both algae and zooplankton, a phytoplankton bloom initially may retard zoeal development; however, following the increase of the herbivore population, more nutritionally adequate food is available and would accelerate larval development. Do the low-salinity Columbia River plume and other river effluents effectively act as barriers against northerly alongshore transport of larvae? The lower temperatures and salinities in 1971, particularly in the nearshore area, coupled with adverse biological pressures, i.e., increased predation, may have had a synergistic effect on larval mortality. Many alternatives are open in marine ecosystems where stochastic processes prevail producing innumerable permutations. The indirect effect of physical variables on larval food organisms and predator-prey relations can be extremely complex and important. Subtle changes in these relations may have an accumulative effect on a larval population already in a stressed condition and near the point at which recovery diminishes.

Answers to these questions remain conjectural and may only be sought through further comprehensive and detailed studies. However, in conclusion, there is no substantial evidence from this study that the colder winter of 1971 caused a delay in the initial appearance and developmental schedule throughout the larval period of *C. magister*. The generally poor appearance of the early zoeal larvae collected during the 1971 season suggests that whatever factor(s) responsible for the apparent mortality appeared to have an immediate effect on these stages. The first few zoeal stages may be the critical period in the early life history of *C. magister* where the greatest mortality occurs ultimately determining future year class strength.

RECOMMENDATIONS FOR FUTURE RESEARCH

Studies to date have provided a broad overview of knowledge concerning the initial timing, abundance, and dispersal of *C. magister* larvae in relation to major oceanographic events off the central Oregon coast. First approximation estimates of length of larval life, mortality, and feeding have been achieved, but we are still lacking detailed insight into the dynamics of the larvae-plankton-environment matrix. This study points out our limited knowledge and understanding of the physical and biological mechanisms affecting the dispersal and subsequent survival of *C. magister* larvae. An understanding of these processes is necessary for an understanding of the stability and long-term productive potential of the Dungeness crab as a fishery resource in the Pacific Northwest. By studying processes controlling the dispersal and survival of the larvae, we

may be able to gain insight into stock-recruitment relations and be able to predict the effects of long-term environmental changes. Some specific recommendations for further work are listed below.

1. A minimum of three surveys should be conducted between late January and early June to monitor initial hatching, production, rate of development, and dispersal of the larvae. It is imperative that survey coverage be extended along the Oregon coast to observe patchiness and alongshore dispersal. A grid of stations to within 30 miles of the coast from at least Cape Blanco, Oreg. to Cape Flattery, Wash. is recommended. A sufficient time series of data is required to adequately assess yearly changes in the larval populations in order to gain insight into mortality processes. Also, a long-term series is needed as a background of knowledge upon which more specialized short-term studies can be based. Six or seven years of plankton sampling seems to be a minimum time series for establishing trends, although 10-15 yr are required to substantiate significant differences.
2. Intensive close-order grid sampling on a short-term basis, following a fairly well-defined and homogeneous "patch" of larvae, should be conducted to assess in more detail mortality and feeding in good and poor areas.
3. This study emphasizes the need for more detailed oceanographic studies in the nearshore environment and how they affect the population dynamics of organisms living in this zone. In conjunction with larval surveys, circulation studies should be expanded during the winter and spring along the Oregon coast to improve the basis for predicting and evaluating dispersal, primary productivity, etc. A continuous program of temperature, salinity, and current measurements are needed of the nearshore currents during the larval period from January through June and particularly the timing and extent of the March-April transition of the Davidson Current.
4. Short-term exposure of the larvae to environmental variables such as low salinity in combination with varying temperature, food density, etc. and subsequent transfer to optimum conditions for long-term observations in the laboratory are needed to properly evaluate the effects of these factors.
5. Detailed descriptions of the three-dimensional composition of the associated plankton communities are needed in terms of the dominant species, size categories, and diurnal variability. Investigations into the contagious distribution of these organisms, mechanisms of initiation and destruction, are central to understanding prey-predator interaction and attempts to model these phenomena.
6. Fine-mesh (0.165 and 0.053 mm) sampling with the 0.2-m bongo nets should be used concurrently with the 0.7-m bongo nets to examine and answer the questions of food composition and availability utilized by early *C. magister* larvae. In particular, the invertebrate component for both coarse- and fine-mesh samples should be analyzed initially between contrasting years or areas of larval abundance. The use of plankton pumps may be more amenable in this case as fine-mesh nets clog rapidly.
7. The vertical distribution and diurnal movements of *C. magister* larvae throughout its pelagic life is especially important in regard to sampling variability, dispersal, and feeding, and should be studied. Do most of the older zoeal larvae, in fact, reside within a few meters of the bottom in the shallow inshore area?
8. Laboratory studies should be undertaken to analyze the phototactic behavior of the larvae at various stages of development to gain a better understanding of their diurnal movements as may be modified by temperature, hunger state, presence of prey and predators, etc.
9. A new approach is needed in the analysis of larval gut contents. Biochemical techniques of gut material may be used to identify food organisms utilized by the larvae. Energy budgets should be constructed to determine minimum food requirements of the various larval stages. Condition factors indicative of the physiological well-being of larvae may be used to evaluate good versus poor areas and years of feeding.
10. Potential predators that cooccur with *C. magister* larvae should be identified and ingestion rates determined from field and laboratory experiments in order to estimate

their effect on the larval population. Transitional experiments should be carried out in the field to further assess the reality of laboratory studies.

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APPENDIX

TABLE 1. —*Cancer magister* larval abundance for 1970-71 seasons and associated environmental data used in analyses of multiple covariance.

Date	0.2 m-bongo net sampler mesh size (mm)	Larval abundance[1]	Surface temp. (°C)[2]	Surface salinity (‰)
1970:				
1/29	0.571	4,598	10.3	29.55
	0.233	2,607		
2/13	0.571	6,721	11.0	30.25
	0.233	13,276		
2/25	0.571	65	11.4	30.62
	0.233	152		
3/9	0.571	536	10.8	30.99
	0.233	381		
4/16	0.571	88	9.7	33.06
	0.233	0		
4/27	0.571	7,713	9.5	32.98
	0.233	5,267		
5/1	0.571	1,868	9.5	32.98
	0.233	1,847		
5/6	0.571	89	9.2	32.98
	0.233	39		
5/22	0.571	1,817	11.8	32.51
	0.233	1,697		
6/4	0.571	74	9.1	33.62
	0.233	32		
6/23	0.571	0	7.9	33.60
	0.233	26		
7/2	0.571	21	12.5	32.84
	0.233	38		
7/16	0.571	56	9.6	32.73
	0.233	28		
7/29	0.571	0	12.7	32.63
	0.233	0		
1971:				
1/18	0.571	736	9.9	29.50
	0.233	1,007		
2/3	0.571	1,762	8.6	31.80
	0.233	1,930		
2/16	0.571	2,539	9.3	31.00
	0.233	3,408		
3/20	0.571	205	8.5	32.16
	0.233	21		
3/30	0.571	305	8.9	30.81
	0.233	316		
4/22	0.571	390	9.6	32.45
	0.233	999		
5/03	0.571	0	10.4	30.74
	0.233	0		
5/14	0.571	0	11.5	31.76
	0.233	0		
5/29	0.571	26	8.8	33.69
	0.233	25		
6/2	0.571	0	10.1	33.52
	0.233	0		
6/12	0.571	0	13.4	30.04
6/28	0.571	0	15.1	30.75
7/6	0.571	20	11.7	31.83
7/21	0.571	0	9.0	33.53

[1]Number of larvae per 4,000 m^3. Larvae summed over four inshore stations: NH01, NH03, NH05, NH10.
[2]Averaged values over four inshore stations.

SUBTIDAL AND INTERTIDAL MARINE FOULING ON ARTIFICIAL SUBSTRATA IN NORTHERN PUGET SOUND, WASHINGTON[1]

CHARLES H. HANSON[2] AND JONATHAN BELL[3]

ABSTRACT

The design and siting of power plant cooling systems requires detailed information concerning the fouling tendencies of specific organisms on specific construction materials. This study, conducted in the vicinity of Kiket Island, northern Puget Sound, Wash., attempts to provide some of this information.

The sessile community characteristics of five materials exposed at three depths and two locations in the subtidal zone, and of one material in the intertidal zone are described. The degree of biofouling was least for copper-nickel alloy and progressively greater for Plexiglas, wood, steel, and concrete. Media decay and biological accumulation was greatest at the near-surface level, decreasing in intensity with increasing depth. The maximum rate of colonization occurred during the late spring (April-June) and early fall (mid-August-October). The present study, an analysis of biofouling, indicates that if the proposed power plant were to be built at Kiket Island, its cooling system intake should be sited in water deeper than 6 m and should have a safe and adequate fouling control scheme.

The settlement of entrained fouling organisms seriously affects the proper functioning of industrial cooling systems (Dobson 1946; Beauchamp 1966; Holmes 1970). Thus, the design of a cooling system requires detailed information concerning the fouling tendencies of specific organisms on specific construction materials. The present study — conducted in the vicinity of Kiket Island, northern Puget Sound, Wash. — attempts to provide some of this information. At the time, the study area was the proposed site for a 1,000 MW nuclear power plant with a once-through cooling system.

The study analyzed the fouling resistances of several common construction materials both in the subtidal and in the intertidal zones. Colonization in the subtidal zone was examined from April to November 1972, while colonization in the intertidal zone was examined from December 1971 to September 1972. Short-term (series I) and long-term (series II) exposures of test materials provided information about the rate of fouling accumulations and progressive community change. The study also determined the seasonal and vertical distribution of the dominant fouling organisms endemic to the Kiket Island area. These exposures also allowed a determination of the periods of maximum colonization by fouling organisms.

MATERIALS AND METHODS

Subtidal Fouling

Two test sites for the study of subtidal fouling were established offshore from Kiket and Skagit islands (Figure 1), in water of a mean depth of 18 m. At each test site five construction materials were tested for their resistances to fouling. The materials that were tested included a 90% copper-10% nickel alloy, steel, Plexiglas[4] (an acrylic plastic), white pine wood, and concrete. The materials were cut into 10 cm × 10 cm squares—54 squares each of steel, Plexiglas, and wood; 18 squares each of copper-nickel alloy and concrete. The squares or "plates" had two 12.7-mm holes drilled into opposite corners of the plate. Rope was threaded through the holes and the plates were then separated into 18 "test panels"—each panel having three plates of steel, Plexiglas, and wood, and one plate of copper-nickel alloy and concrete. Within each panel there was a random distribution of plates.

The test panels were suspended in the water at mean depths of 1, 6.1, and 15.3 m below the sur-

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[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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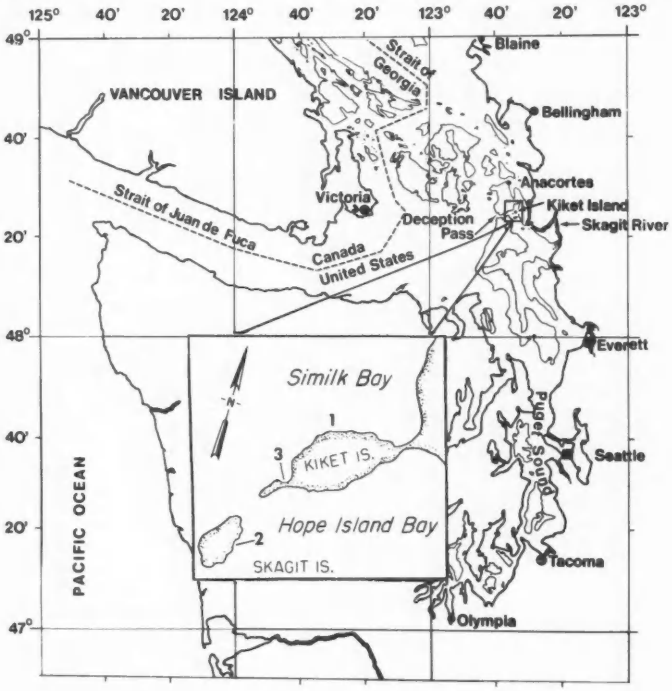

FIGURE 1. — Map of western Washington, with the study areas shown in inset: 1) Kiket Island subtidal site; 2) Skagit Island subtidal site; and 3) intertidal site.

face. The 1-m depth test panels were suspended from a steel surface float. The 6.1- and 15.3-m depth test panels were suspended between a concrete bottom anchor and a steel float moored just below the extreme low water level. At both test sites three panels were deployed at each depth (Figure 2).

Series I test panels were exposed for periods of 41 and 79 days offshore from Skagit Island and were exposed for 58 and 101 days offshore from Kiket Island. Series II test panels were exposed continuously for a period of 8 mo (16 April-29 November 1972) at both locations.

The standard analytical procedure for series I plates involved identification of the organisms, estimation of the percent of plate coverage, and, if possible, a measurement of the size of the organisms. A central square of each plate, measuring 7 cm × 7 cm, was used for analysis. The fouling organisms on each 49-cm² central area were scraped onto preweighed filter paper, dried at approximately 100°C for 24 h, and then weighed to 0.01 g. Monthly qualitative observations of series II plates, anchors, lines, and floats were made using scuba.

Intertidal Fouling

An examination was made of the settling rate of intertidal fouling organisms on concrete slabs. The concrete slabs measured 38 cm wide by 76 cm long by 15 cm deep. The slabs were uniform in texture, composition, surface configuration, stability, and resistance to wave action. They were anchored to the beach with steel reinforcing bars imbedded in the concrete. The long dimension was parallel to the water and the top surface was placed horizontal to the plane of the water. The slabs were positioned at the +0.6-, 0-, −0.6-, and −1.2-m water levels relative to mean sea level. Once each month the density of the fouling organisms was determined from a series of randomly chosen 49-cm² areas on each concrete slab.

RESULTS

Physicochemical Environment

Seasonal water quality data for the Kiket Island area have been described in detail (Stober et al.

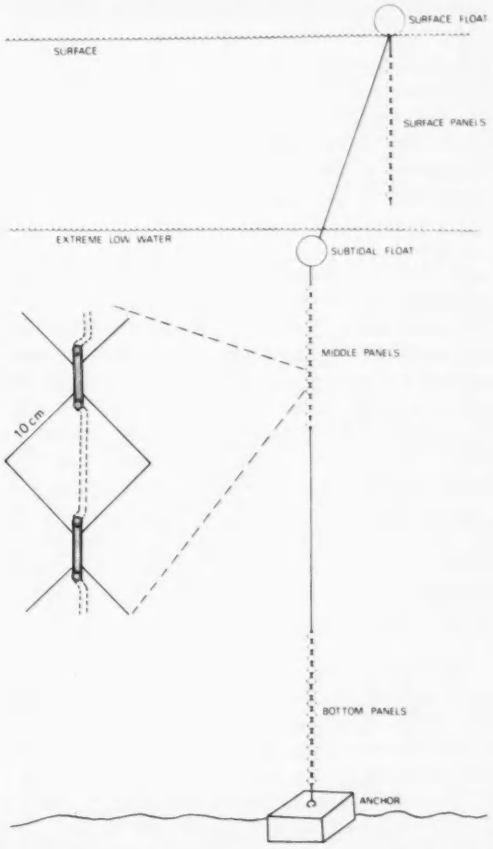

FIGURE 2.—A schematic of the array of subtidal test panels used to measure biofouling with inset showing details of test plate attachment.

1973). Weekly minimum, mean, and maximum temperature and salinity readings are presented in Figure 3. Average weekly temperatures ranged from 6.2°C to 11.8°C. Average weekly salinities ranged from 17.5 to 29.7 g/liter; pH ranged from 7.1 to 8.2; and dissolved oxygen concentrations ranged from 10.5 to 13.3 mg/liter. Lincoln et al. (1970) and Bendiner et al. (1972) have detailed the physical oceanography and vertical stratification of the Kiket Island area. The physicochemical characteristics of North Skagit Bay led Stober et al. (1973) to classify the study area as a well mixed estuary.

Qualitative observations of the study area were made periodically while scuba diving. The bottom in the vicinity of the fouling plates at Kiket Island consisted of soft silt and sediment with a few rock outcroppings. Acorn barnacles, *Balanus crenatus*, densely covered the few rock outcroppings, but were otherwise not present. At a depth of 18 m, light penetration was low and bottom currents appeared to be generally slow. In contrast, the bottom at Skagit Island was virtually free of silt and was predominantly covered with cobble and rock outcroppings. The cobble and rock were densely covered with *B. crenatus*. At 18 m, light penetration was moderate and the bottom currents were consistently more rapid than those at the Kiket Island site.

Fouling Colonization of the Construction Materials

The fouling resistances of the different test materials were compared using the dry weights of organisms collected during periodic sampling. The dry weight data for the 1-m level are shown in Table 1. Weight data of the removable material from the 15.3-m and 6.1-m levels were negligible except for the plates of wood and concrete colonized by *Balanus crenatus* (Table 2).

COPPER-NICKEL ALLOY.—There was no removable material through the first 58 days. The

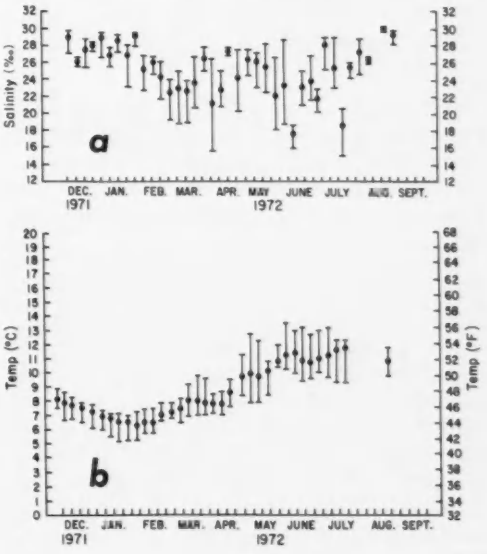

FIGURE 3.—Weekly mean, minimum, and maximum salinity measurements (a) and water temperature (b) recorded in the Kiket Island area (data from Stober et al. 1973).

TABLE 1.—Dry weight in grams of material collected per square centimeter of surface area from five artificial media exposed at the near-surface level for four time periods.

Exposure	Copper-nickel alloy	Steel	Plexiglas	Wood	Concrete
May 26					
41-day exposure	0.00	0.15	0.19	0.13	0.12
June 12					
58-day exposure	0.00	0.26	0.09	0.09	0.07
July 3					
79-day exposure	0.01	0.23	0.08	0.07	0.05
July 25					
101-day exposure	0.01	0.13	0.04	0.05	0.04

TABLE 2.—Density of the barnacle, *Balanus crenatus*, per square centimeter of surface area collected from five artificial media at three depths.

Exposure and depth	Copper-nickel alloy	Steel	Plexiglas	Wood	Concrete
May 26					
41-day exposure					
1 m	0.0	0.0	0.0	0.0	0.0
6.1 m	0.0	0.0	0.0	0.0	0.0
15.3 m	0.0	0.0	0.0	0.0	0.0
June 12					
58-day exposure					
1 m	0.0	0.2	0.1	0.2	2.9
6.1 m	0.0	0.1	0.4	0.3	1.6
15.3 m	0.0	0.0	0.0	0.0	0.4
July 3					
79-day exposure					
1 m	0.0	0.3	0.8	0.4	4.9
6.1 m	0.0	0.0	0.5	4.6	11.3
15.3 m	0.0	0.0	0.0	39	64
July 25					
101-day exposure					
1 m	0.0	0.1	0.2	0.9	2.1
6.1 m	0.0	0.0	0.0	0.0	0.4
15.3 m	0.0	0.0	0.0	0.1	0.0

79-day and the 101-day samples had removable material weighing less than 0.01 g/cm². Removable material consisted primarily of diatoms, with small deposits from flaking of the alloy surface. No mussels, barnacles, or green algae were observed.

STEEL.—After 41 days the dry weight of the removable material was 0.15 g/cm², after 58 days 0.26 g/cm², after 79 days 0.23 g/cm², and after 101 days 0.13 g/cm². A high proportion of the removable material was rust; biological accumulations consisted of diatoms, barnacles, green algae, and mussels. *Balanus crenatus* densities at the 1-m depth ranged from 0.0 on day 41 to 0.3/cm² on day 79. *Balanus* density at the 6.1-m level ranged from 0.0 on day 41 to 0.1/cm² on day 58. No *Balanus* were found at the 15.3-m level.

PLEXIGLAS.—After 41 days the dry weight of the removable material was 0.19 g/cm², after 58 days 0.09 g/cm², after 79 days 0.08 g/cm², and after 101 days 0.04 g/cm². Removable material consisted of diatoms, green algae, and barnacles. Mussels were not observed on the Plexiglas media. The density of *Balanus crenatus* at the 1-m level ranged from 0.0 on day 41 to 0.8/cm² on day 79. At the 6.1-m level *Balanus* densities ranged from 0.0 on day 41 to 0.5/cm² on day 79. No *Balanus* were found at the 15.3-m level.

WOOD.—After 41 days the dry weight of the removable material was 0.13 g/cm², after 58 days 0.09 g/cm², after 79 days 0.07 g/cm², and after 101 days 0.05 g/cm². Removable material consisted primarily of diatoms and barnacles with small amounts of green algae. No mussels were found. The density of *Balanus crenatus* at the 1-m level ranged from 0.0 on day 41 to 0.9/cm² on day 101. *Balanus* density at the 6.1-m level ranged from 0.0 on day 41 to 4.6/cm² on day 79. *Balanus* density at the 15.3-m level ranged from 0.0 on day 41 to 39/cm² on day 79. *Balanus* achieved 100% of plate coverage on day 79 at the 15.3-m level. No wood borers were found at any level.

CONCRETE.—After 41 days the weight of the removable material was 0.12 g/cm², after 58 days 0.07 g/cm², after 79 days 0.05 g/cm², and after 101 days 0.04 g/cm². Removable material consisted of diatoms, barnacles, mussels, and green algae. The density of *Balanus crenatus* at the 1-m level ranged from 0.0 on day 41 to 4.9/cm² on day 79. *Balanus* density at the 6.1-m level ranged from 0.0 on day 41 to 11.3/cm² on day 79. *Balanus* density at the 15.3-m level ranged from 0.0 on day 41 to 64/cm² on day 79. *Balanus* achieved 100% plate coverage on day 79 at the 15.3-m level. Bay mussels, *Mytilus edulis*, achieved a density of 0.4/cm² at the 1-m level — none were found in the deeper water samples.

Intertidal Fouling

The colonization of fouling organisms was observed on concrete test slabs positioned at various levels in the intertidal zone of Kiket Island. The principal algae species colonizing the slabs were *Fucus distichus* and *Ulva lactuca*. The dominant animal species included the acorn barnacle, *Balanus glandula*, and the bay mussel. A detailed examination of the natural vertical and seasonal distribution of the intertidal flora and fauna of Kiket Island is presented by Houghton (1973).

Settlement by barnacles (Figure 4) was the most rapid during late May. Barnacle density peaked in June, but subsequently there was a general decrease in the density—probably due to intraspecific competition for the limited growing area. Barnacle settlement was most successful at the −0.6-m level. There was limited settlement at the —1.2-m level and at the 0.0-m level. No barnacles successfully settled at the +0.6-m level.

Settlement by barnacles at the −1.2-m level appeared to be limited by heavy siltation and diatomaceous growth. The absence of barnacles at the +0.6-m level was principally caused by the extensive exposure of the organisms to sunlight. Successful settlement at the −0.6-m level was the result of a limited exposure to sunlight and of the moderate wave action limiting the silt/diatom buildup.

Settlement by *M. edulis* was predominant at the −0.6-m level, where maximum density was 1.3/cm². *Mytilus edulis* were present in lower densities at the 0.0-m and −1.2-m levels. The same factors affecting settlement by barnacles—exposure to sunlight and the silt-diatom buildup—affected settlement by *M. edulis*. Mussels were observed to attach primarily in the late summer and in the fall (July-October); a few individuals were observed in April and May.

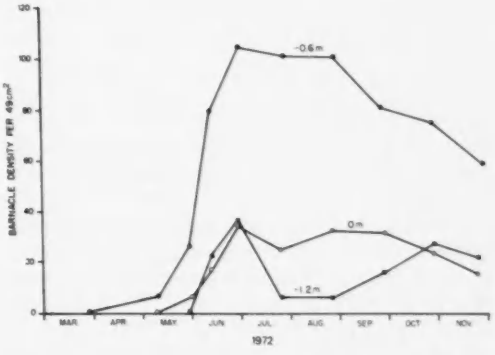

FIGURE 4.—Mean density of *Balanus glandula* attached to concrete substrata exposed in the intertidal zone of Kiket Island (tidal level relative to mean sea level).

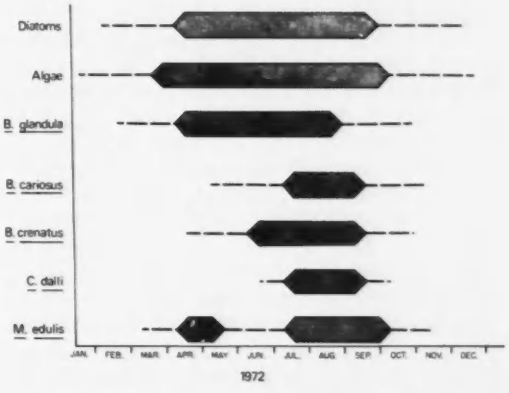

FIGURE 5.—Seasonal distribution of predominant subtidal and intertidal fouling organisms.

Seasonal Distribution of Fouling Organisms

The seasonal distribution of the major sessile fouling organisms found in the Kiket Island area is presented in Figure 5. Conclusions about the distribution of these organisms are based on data collected during a 1½-yr study of intertidal settlement and an 8-mo study of subtidal fouling. Comparable conclusions were reached by DePalma (1966) for Admiralty Inlet.

The first diatoms to appear on the study plates were those of the genus *Melosira*. These diatoms remained dominant throughout the study period. *Navicula* and *Fragilaria*, as well as a large number of unidentified diatoms, also settled on the plates, but were not nearly as abundant as *Melosira*. Although the spores of many diatom species were present all year, settlement occurred predominantly from early spring to midsummer.

Four dominant forms of algae settled on the study plates. *Fucus distichus* and *Ulva lactuca* were dominant in the intertidal zone, while *Ulothrix* sp., *Cladophora* sp., and *Ulva lactuca* were dominant in the subtidal zone. The algae was abundant seasonally—in the spring and summer there was an extensive algal cover on the plates, yet in the fall and winter months the abundance of algae decreased substantially. Many small crustaceans, including copepods, cladocerans, and amphipods, were observed inhabiting the diatoms and algae covering the test plates.

Although barnacles of the genus *Balanus* were present throughout the year, their rate of settlement varied greatly with the different seasons. As a general rule, maximum settlement occurred during the late spring (April-June) and in early fall (mid-August-October). For example, *B. glandula* settled in the intertidal zone from February

through November, but the maximum rate of settlement was observed in May and August. However, in the subtidal zone, *B. crenatus* settled from April to November, but with a peak in late July and early August. Others, like *B. cariosus* and *Chthamalus dalli,* settles sporadically from May to November and peaked in August and September.

Settlement by the bay mussel occurred primarily from August to November, although there was some settlement during April and May. It appears that prior settlement by diatoms, algae, and barnacles is necessary for the establishment of a mussel colony. Cleaned test plates were exposed in both the intertidal and the subtidal zones and were compared with plates already having an established community of diatoms, algae, and barnacles. Only on those plates which were already fouled was there any settlement by mussels. Coe (1932) reported the same phenomenon and concluded that the smooth quality of nonfouled surfaces was not suitable for attachment by the byssus of young mussels.

Vertical Distribution in the Subtidal Zone

At both subtidal test sites there was a distinct vertical pattern to the fouling of the test plates. The greatest number of species settled at the near-surface (1-m) level. At that level there were colonial diatoms of the genera *Melosira, Navicula,* and *Fragilaria,* and three species of the acorn barnacle, *Balanus crenatus, B. glandula,* and *B. cariosus*. Subdominant genera included the green algae, *Ulothrix, Ulva,* and *Cladophora*. Small numbers of the bay mussel were also found at the surface level. At the middle depth (6.1 m) the species composition of the fouling organisms changed. Green algae became rare and diatoms were less dense. *Mytilus edulis, B. glandula,* and *B. cariosus* were absent. *Balanus crenatus* increased in density with increasing depth at Skagit Island, but not at the Kiket Island site.

The 15.3-m level was very different from the two upper levels. The plates had no algae or diatoms. *Balanus crenatus* was the dominant species. Consistently higher densities of *B. crenatus* were observed at the Skagit Island test site. The ratio of densities between Skagit and Kiket Island for *B. crenatus* at the 15.3-m level ranged as high as 50 to 1 for the wood and concrete test plates.

DISCUSSION

Marine fouling presents one of the most serious long-term operational problems for power generating stations using saline waters for cooling (Powell 1933; Dobson 1946; Holmes 1970). Fouling accumulations reduce the carrying capacity of cooling system conduits by increasing the frictional resistance and by reducing the pipeline diameter. In addition, marine fouling reduces the heat transfer efficiency of steam condenser systems and promotes severe corrosion of the condenser system components. The accumulation of fouling debris, such as dead shells, adds to the inefficiency by clogging the condenser tubes.

Data are needed by design engineers in order to determine the probable construction requirements for the control of fouling in a power plant cooling system. Because marine fouling varies considerably from one location to another, an on-site determination of the population dynamics of fouling organisms is desirable. Each site should be studied in order to determine: 1) the species composition of sessile organisms colonizing specific construction materials at various subtidal levels, 2) the types of construction materials least likely to be fouled, 3) the seasonal variations in settlement and abundance, and 4) the times of the year when antifouling procedures must be considered. The present study was, in a sense, an attempt to study all these factors, and although the power plant for which the study was intended may never be built, this report should be a useful guide to future studies of power plant siting.

Data for the present study were collected from test plates suspended at various depths in the water. However, caution must be used in extrapolating studies carried out with these small static test plates. Graham and Gay (1945) reported that plates, 9.8 cm × 9.8 cm, were found to give results just as reliable as larger ones. Holmes (pers. commun.), however, considers that "edge effects and top-to-bottom gradients could be very important in biassing results from such small panels." Although no effort was made in the present study to determine the reliability of the small plates, a 3-cm border zone surrounding the 49-cm² examination area was considered sufficient to eliminate any edge effect. There was consistently less than 10% variation in the dry weights of the removable material and in the density of barnacles taken from different plates of the same media at the same water level.

One must also recognize that data collected from static test panels can only give a limited indication of the growth rate of fouling organisms in a continuous-flow cooling system (Dobson 1946). Fouling organisms naturally dependent upon water currents to supply food, may have their growth rates enhanced by the greater water velocities of a continuous-flow cooling system (Dobson 1946; Benson et al.[5]). Mawatari[6] observed, however, that test panels exposed in current velocities of 4 to 7 m/s remained totally free of fouling organisms. Efforts to reduce the influence of static plates have been made by several authors (Smith 1946; Doochin and Smith 1951; Wood 1955), but these efforts have produced conflicting results.

Several additional factors should be mentioned which influence both the growth rate and the species composition of sessile organisms colonizing test plates. The larvae of barnacles and many other fouling organisms have been found to be negatively phototrophic when they attach to a surface. Therefore, these organisms prefer to attach to shaded or dark surfaces (Visscher and Luce 1928; Thorson 1964). Also, surface texture has been shown to affect the rate of attachment of settling larvae (Crisp and Ryland 1960; Pomerat and Weiss[7]). In general, porous and rough surfaces have the greatest fouling accumulation.

All of these factors influenced the results obtained by the present study. For example, the test plates, although they were subjected to natural flow currents of the marine environment, were not subjected to the "unnatural" flow currents of a power plant cooling system. Thus, fouling on the test plates might be somewhat different from the fouling of a cooling system. Yet the test plates offer useful indications as to what will happen in the actual cooling system and therefore they are useful for predictive planning of power plant engineers.

In the present study, variations in the abundance and species composition of fouling organisms were observed for the different construction materials. Accumulation was slow on the copper-nickel alloy plates, but was rapid and complete on the concrete and wood plates. Because the fouling plates were exposed to identical environmental conditions, the differences in fouling resistance must have been dependent upon the differences between the media. Previous research has shown the same results—Woods Hole Oceanographic Institution (1952), for example, found that copper-nickel alloy maintains its fouling resistance for 10 mo, much longer than concrete or wood.

Depth was found to have a significant effect upon the rate of fouling accumulation. For example, the dry weight of removable material from all materials placed below the surface level (1 m) was negligible except for those wood and concrete plates colonized by *Balanus crenatus*. Yet at the surface there was considerable algal and diatomaceous growth on all media except the copper-nickel alloy. The only organism which increased in density as the depth increased was *B. crenatus*, the only organism colonizing the plates at the 15.3-m level. Because these results were similar for all media and because they were corroborated by qualitative examinations made on the ropes, floats, and anchors, it appears that a cooling system intake in the Kiket Island area should be sited in water deeper than about 6 m. Based on biofouling results, the cooling system intake should not be sited at the surface because fouling is greatest at that level.

An analysis of the seasonal distribution of the fouling organisms showed that there was initially an accumulation of brown detrital film and bacterial slime on the fouling plates. Soon a filamentous algae, *Enteromorpha*, and a diatom, *Melosira*, became established. As floral density increased, greater numbers of Crustacea were observed living in the growths on the plates. Barnacle and mussel colonization of the test plates occured throughout the year, but was greatest from April through October. For mussels, at least, it appeared that a previous accumulation of fouling material was required before the mussels would attach to the test plates. Thus, it would appear that fouling control should be greatest during the spring, summer, and early fall. During late fall and winter fouling control need not be so greatly emphasized. It must be remembered that the time for maximum fouling may vary from year to year, and thus fouling control should be regulated by routine observations of larval settlement. In addition, early fouling control may help to deter col-

[5]Benson, P. H., E. L. Littauer, and N. P. Stumbaugh. 1968. Outlook for marine corrosion and fouling protection. Paper presented at Symposium on Ocean Technical Problems of the 1970's. 61st Annu. Meet., Los Ang., Calif., Dec. 1968, 42 p.

[6]Mawatari, S. 1965. Protection of power plants from biological fouling. Unpubl. rep. Research Institute for Natural Resources, Tokyo, Jap.

[7]Pomerat, C. M., and C. M. Weiss. 1946. The influence of texture and composition of surface on the attachment of sedentary marine organisms. Unpubl. manuscr.

onization by mussels, which, according to Hoshiai (1964) and Holmes (1970), are the principal fouling organisms in power plant cooling systems.

The use of intermittent chlorination as a fouling control agent has been noted by Holmes (1970), Morris (1971), and Draley (1972). In general, most investigators feel that the larvae of various marine fouling organisms are more sensitive to chronic low-level concentrations of chlorine than are the adults (Dobson 1946; Turner et al. 1948). Thus, greatest effectiveness results from repeated low-level chlorination, which either kills the larvae directly or creates an unfavorable environment for settlement.

Any fouling control scheme should maintain adequate precautions against excessive interference with organisms inhabiting the receiving water ecosystem. Chemical toxins such as chlorine are objected to as antifouling agents primarily because of the possible detrimental effects on nontarget organisms (Waugh 1964; Hamilton et al. 1970; Stober and Hanson 1974). This effect is particularly true when the treated effluent is discharged directly into the aquatic environment.

The data presented in this study can only be called preliminary. Additional tests should be run which would include at least one complete annual cycle study of subtidal fouling. Yet the present study does indicate that if the proposed plant were to be built at Kiket Island, its cooling system should be in water deeper than 6 m and should have a safe and adequate fouling control scheme. Of the different construction materials tested in this study, it would appear that copper-nickel alloy would most effectively deter fouling and that concrete and wood would be least effective.

It must be emphasized that the present study is an analysis of biofouling. Prior to the siting and final design of the cooling water intake structure, consideration must also be given to the potential effects of entrainment on zooplankton and larval and juvenile fish.

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OBSERVATIONS ON THE FISH FAUNA ASSOCIATED WITH OFFSHORE PLATFORMS IN THE NORTHEASTERN GULF OF MEXICO

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ABSTRACT

The fish fauna associated with two U.S. Navy research platforms, Stage I and Stage II, in the northeastern Gulf of Mexico off Panama City, Fla., was studied at irregular intervals from 1970 to 1974. Such platforms function as artificial reef habitats and support diverse and abundant fish populations not normally characteristic of the open sandy bottoms in the area.

A total of 101 taxa (identified to family or species) was recorded at the two platforms; 61 species were observed at Stage I in water 32 m deep and 86 taxa at Stage II in water 18 m deep. The greater number of species recorded at the shallower location may be more a result of the greater number of observations made there than of differences in the two habitats. The number of species present at the platforms varies considerably at different times of the day and year. Species numbers are greatest during the summer and fall, but many species begin to move offshore or southward as the water temperature drops, and only about 50-60% of those recorded at the platform remain in December. The number of species diminishes to about 16% in February at Stage II, then increases gradually with the rising water temperature in the spring.

Major species occupying the platform habitats include fishes usually characteristic of pelagic, inshore (coastal or estuarine), and rocky reef environments. At the platforms, the pelagic species and most of the larger predators occupy various levels of the water column, either directly below or surrounding the structure, while most of the other species are associated either with the pilings and cross-members of the platform or with the bottom. For some of the species, the platform provides food and shelter, while for others, it offers only shelter. Some species may be present only to feed on the numerous fishes and other organisms concentrated there. Diel rhythms of activity are obvious for many of the fishes, with some species active only during the day, and others only at night.

Offshore oil drilling platforms are known to attract various species of marine fishes and thus function as artificial reefs (Carlisle et al. 1964; Treybig 1971). Anglers often recognize such platforms as desirable fishing sites. Carlisle et al. (1964) documented the development of fish populations (as well as populations of encrusting organisms) at two platforms constructed off the coast of California. The supporting piles and cross-members of such platforms provide hard substrates for the settling of pelagic larvae of encrusting invertebrates and algae which, with their associated invertebrate populations, provide food and shelter for reef fishes attracted to the structures. In addition, many pelagic fishes congregate about these platforms, attracted either by the solid, reeflike nature of the supporting structures, or by the numerous smaller forage organisms in the area.

Many comparable platforms have been constructed in the Gulf of Mexico since the 1940's, but no studies of their associated fish faunas have been reported, even though they are known to attract numerous species of fishes. Current studies by personnel of the University of Southwestern Louisiana have documented the fish fauna of drilling platforms off the coast of Louisiana (Sonnier et al. 1976). This paper records the fish populations observed around two offshore platforms in the northeastern Gulf of Mexico off Panama City, Fla.

LOCATION AND TIME OF STUDY

Two research platforms operated by the U.S. Navy off the coast of Panama City are referred to as Stage I and Stage II. Stage I is 17.7 km offshore in water 32 m deep (lat. 30°00.5'N, long. 85°54.2'W). Stage II (Figure 1) is 3.2 km offshore in water 18 m deep (lat. 30°07.2'N, long. 85°46.4'W). The pilings of Stage I form a square on the sea bottom with each side measuring 32.6 m, whereas those of Stage II measure 19.1 m. The two platforms were the sites of biofouling studies

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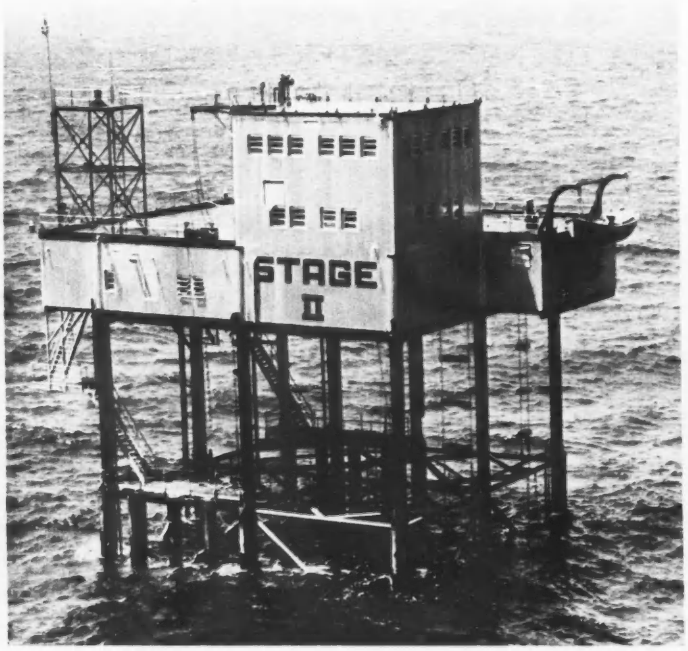

FIGURE 1.—Stage II, the Navy research platform 3.2 km offshore of Panama City, Fla. (U.S. Navy photo.)

by Pequegnat et al. (1967), Pequegnat and Pequegnat (1968), and Culpepper and Pequegnat (1969). Vick (1964) mentioned 13 species of fishes either collected or reported from the stages and vicinity.

These platforms were examined occasionally from 1970 to 1974 by the first and second authors in connection with studies of reef fishes in the northern Gulf of Mexico. During the fall of 1970 (Ogren) and summer of 1972 (Hastings and Mabry), the authors participated in the Scientist-in-the-Sea (SITS I and II) diving program at the Naval Coastal Systems Laboratory in Panama City and were able to make repeated observations at the platforms.

Between September 1970 and January 1974, 10 dives were made at Stage I (including 1 night dive) and 21 dives were made at Stage II to determine the composition of the fish populations under the structures (see Tables 1, 2). During the SITS II program in 1972, a series of dives made at various times during four consecutive 24-h periods (1-4 August) enabled us to determine diel patterns of concentration of fish schools around and under the platforms.

METHODS

During each dive an attempt was made to identify each species of fish present in the area and to estimate its abundance. At the end of a dive a debriefing session was held and notes were compared as to species and numbers observed. Divers often carried hand nets or spears for collecting unusual or difficult to identify species.

Dives were usually conducted on an irregular basis, and the length of the observation period and the area examined varied considerably from one dive to the next. Consequently, no numerical values were assigned to these estimates of abundance. Instead, relative terms such as few, several, common, and abundant were used, simply to indicate the impression received by the divers as to the numbers of each species present. It should be kept in mind, however, when considering these estimates, that such relative terms may have different meanings when applied to different species of fishes. For example, an absolute number such as 100 individuals might be interpreted as few if applied to a schooling species such as *Harengula pensacolae*, but as abundant if applied to a soli-

tary reef species such as *Chaetodon ocellatus*. These estimates (recorded for all dives in Tables 1 and 2) are admittedly subjective but may be useful in describing the seasonal changes in the fish populations around the platforms.

Our dives at Stage II during the SITS II program were scheduled to occur at approximately 5-h intervals from 1 to 4 August 1972. Although this schedule was not always followed because of other diving commitments of the program, we made 10 dives which included at least 2 dives during each quarter of the 24-h day. Times of the dives are presented as Central Standard Time (CST) in this report. During early August 1972, the times of sunrise and sunset at Stage II were approximately 0500 and 1840 CST, respectively.

During the SITS II program, two censusing stations were set up under Stage II: Station 1 on the bottom at 18.3 m; and Station 2 directly above, about 4.6 m below the water surface. Both stations were the same size and were conveniently delimited by the cross-members at one corner of the platform. The stations measured 4.9 × 4.9 × 7.0 m. Counts were restricted to that portion of the water column estimated to extend 1 m upward from the base of the cross-members (corresponding to the bottom at Station 1). Thus, the water volume included within each station was about 12 m^3.

During each dive at the censusing stations the authors attempted to identify and count all species of fishes present within each station. Counts were recorded on plastic slates during the censusing, then transferred to data sheets after surfacing. Times required to make each census varied because of the great variation in the numbers of fishes present, but were usually about 10-15 min for each station. In most cases both stations were censused on each dive, and counts for Station 2 were made about 15-20 min after the counts for Station 1. On dives 1, 9, and 10, only one of the two stations was censused. Some species were so numerous at times that only estimates of their abundance could be made. Such estimates of fish abundance by two divers making counts at the same time were generally in the same order of magnitude.

During nocturnal diving operations, an underwater light was suspended near the surface below a ladder (to facilitate diver return) at the corner of the platform farthest from the censusing stations. It was not visible underwater at the censusing stations and did not appear to affect our counts. Although some fishes were attracted to this light, they were mostly juveniles and larvae of pelagic species.

Nomenclature and arrangement of the families in Tables 1, 2, and 3 follow Bailey et al. (1970).

RESULTS AND DISCUSSION

All species recorded at the two stages during this study are listed in Tables 1 and 2. Table 3 is a list of the species recorded in the two stations at Stage II during the SITS II dives. These tables should be examined in connection with the following synopsis of the results of this study. At least 101 taxa (identified to family or species) were recorded during this study at the two platforms; 61 species were recorded at Stage I during 10 dives, and 86 taxa were recorded at Stage II during 21 dives. The greater number recorded at Stage II is probably primarily a result of the greater number of observations there. In general, the fish faunas of the two stages are quite similar, and most of the species recorded at only one could be expected to occur at both occasionally. Of the 101 taxa recorded, about 75 were frequently observed during the study and could be regarded as characteristic members of the fauna, 41 were recorded as common or abundant. Of the latter group, 27 species were recorded at Stage I and 36 at Stage II.

Faunal Composition

The two stages represent an artificial reef habitat in an area previously characterized by flat sand bottoms. Thus, the fishes inhabiting the stage environment are a mixture of faunal types, including some species usually expected in such flat, sandy areas, but also including many species more characteristic of other habitats of the northern Gulf of Mexico, especially fishes which are attracted to reef environments.

A number of demersal species characteristic of open sand habitats of the northern Gulf of Mexico were frequently recorded at the stages, but these were usually seen over the open sandy areas surrounding the stages. Examples are *Dasyatis* sp., *Raja eglanteria*, *Arius felis*, *Ogcocephalus radiatus*, *Stenotomus caprinus*, *Hemipteronotus novacula*, *Prionotus* sp., *Paralichthys albigutta*, *Lactophrys quadricornis*, and *Chilomycterus schoepfi*. In addition, many species recorded at the stages are pelagic fishes characteristic of open

TABLE 1.—Fishes recorded at Stage I off Panama City, Fla., with estimates of usual abundance and habitat occupied.

Species	Abundance[1]				Habitat[1]
	Spring (Apr.)	Summer-fall (July-Nov.)	Winter		
			Dec.	Jan.	
Carcharhinidae:					
Carcharhinus milberti	—	few	—	—	O
Dasyatidae:					
Dasyatis sp.	—	few	—	—	B
Muraenidae:					
Gymnothorax nigromarginatus	—	few	few	—	B
Clupeidae:					
Sardinella anchovia	—	com-abun	abun	—	U
Ariidae:					
Arius felis	—	sev	—	—	B
Batrachoididae:					
Opsanus pardus	sev	sev	sev	com	B
Antennariidae:					
Antennarius ocellatus	few	few	few	few	B
Ogcocephalidae:					
Ogcocephalus radiatus	—	few	few	few	B
Serranidae:					
Centropristis ocyurus	com	com	com	com	B
Diplectrum formosum	sev	sev-com	sev-com	—	B
Epinephelus nigritus	—	—	—	few	L
Mycteroperca microlepis	—	few-com	few	sev	L
Serranus subligarius	sev	sev-com	sev-com	com	B-P
Grammistidae:					
Rypticus maculatus	—	sev-com	sev	com	B-P
Apogonidae:					
Apogon pseudomaculatus	few	sev-com	—	sev	B
Rachycentridae:					
Rachycentron canadum	—	few	few	—	O-U
Echeneidae:					
Echeneis neucratoides	—	few-sev	—	sev	([2])
Carangidae:					
Caranx crysos	—	com	—	—	U
Caranx hippos	—	sev-com	—	—	O-U
Caranx ruber	—	few-com	few	—	U
Decapterus punctatus	—	com-abun	abun	few	U
Elagatis bipinnulata	—	sev	sev	few	O-U
Seriola dumerili	sev	few-com	com	com-abun	L-O-U
Seriola rivoliana	—	—	few	—	U
Trachurus lathami	—	com	—	—	L
Lutjanidae:					
Lutjanus campechanus	—	few	few	—	L
Lutjanus griseus	few	sev-abun	few	sev	L-U
Rhomboplites aurorubens	sev	com-abun	—	com	L
Pomadasyidae:					
Haemulon aurolineatum	com	com-abun	com-abun	sev	L
Haemulon plumieri	—	—	few-sev	—	L
Sparidae:					
Archosargus probatocephalus	—	few	—	—	U
Lagodon rhomboides	—	sev	—	—	L-U
Sciaenidae:					
Equetus lanceolatus	—	sev-com	—	com	B
Equetus umbrosus	com	sev-com	com	com	B
Equetus sp.[3]	—	few	—	—	B
Kyphosidae:					
Kyphosus sectatrix	—	sev	—	—	U
Ephippidae:					
Chaetodipterus faber	com	sev-com	sev	com	L-U
Chaetodontidae:					
Chaetodon ocellatus	few	few	few	few	B-P
Chaetodon sedentarius	—	few	few	—	B
Holacanthus bermudensis	sev	sev-com	sev	sev	L-U
Pomacentridae:					
Abudefduf saxatilis	—	few-sev	—	sev	P
Chromis enchrysurus	—	few	—	few	B
Chromis scotti	—	sev-com	—	sev	B-P
Pomacentrus partitus	—	few-sev	—	—	P
Pomacentrus variabilis	com	sev-com	sev	com	B-P
Labridae:					
Halichoeres caudalis	com	sev-com	—	few	B
Thalassoma bifasciatum	—	few-sev	—	sev	P
Sphyraenidae:					
Sphyraena barracuda	—	sev-abun	sev	few	O-U
Blenniidae:					
Blennius marmoreus	—	sev	—	—	B-P
Hypleurochilus geminatus	few	few-com	—	—	P

TABLE 1. — Continued.

Species	Abundance[1]				Habitat[1]
	Spring (Apr.)	Summer-fall (July-Nov.)	Winter Dec.	Winter Jan.	
Gobiidae:					
Coryphopterus punctipectophorus	few	few	—	—	B
Ioglossus calliurus	—	sev	—	—	B
Acanthuridae:					
Acanthurus coeruleus	—	—	—	few	P
Scombridae:					
Euthynnus alletteratus	—	sev-com	sev	sev	O-U
Bothidae:					
Paralichthys albigutta	—	few	—	—	B
Balistidae:					
Balistes capriscus	few	few-sev	few	few	L-U
Monacanthus hispidus	—	few-sev	—	—	P
Ostraciidae:					
Lactophrys quadricornis	few	few	few	—	B
Tetraodontidae:					
Canthigaster rostrata	—	few	—	—	B
Sphoeroides spengleri	—	few	—	—	B
Diodontidae:					
Chilomycterus schoepfi	few	few	few	few	B
61 species	21 species	57 species	31 species	32 species	
100%	34%	93%	51%	52%	
Number of observations	1	6	2	1	
Temperature range	17°-20°C	23°-29°C	18°-19°C	18°C	

[1]Abbreviations are as follows: sev-several, com-common, abun-abundant, B-on bottom, L-lower water column, P-on pilings, O-open water around platform, U-middle to upper water column under platform.
[2]*Echeneis neucratoides* on *Epinephelus, Sphyaena, Seriola, Balistes,* and *Caretta.*
[3]*Equetus* sp. - an undescribed species listed by Bullis and Thompson (1965) as "*Equetus* sp. nov." and by Struhsaker (1969) as "Blackbar drum *Pareques* sp. (undescribed)."

waters, which are attracted to solid, reeflike structures. Smaller baitfishes, such as *Harengula pensacolae, Sardinella anchovia, Etrumeus teres, Opisthonema oglinum, Decapterus punctatus, Trachurus lathami,* and *Scomber japonicus,* were abundant at times and formed dense schools under the stages. Klima and Wickham (1971) demonstrated the potential for harvesting commercial quantities of these and other species by attracting schools to artificial structures. In research conducted near Stage II during 1969, they found *Decapterus* and *Sardinella* more numerous than *Harengula,* but did not record the other species. *Harengula pensacolae* was usually the most common species at Stage II during our observations made in 1972, while *Decapterus* and *Sardinella* were more common in other years.

Larger pelagic species often recorded at the stages were *Rachycentron canadum, Caranx bartholomaei, C. crysos, C. hippos, C. ruber, Elagatis bipinnulata, Seriola dumerili, Euthynnus alletteratus,* and *Sphyraena barracuda.* These species were recorded at the stages often enough to indicate some attraction to the structures, even though they are characteristic open-water species. Part of the attraction for these larger predators may be the large number of smaller baitfishes which provide much of their food (Wickham et al. 1973). Publications on the attraction of fishes to artificial reefs have noted that pelagic species such as those listed here are attracted to artificial structures in greatest numbers when the structures extend a considerable distance above the bottom or even reach the surface, as do these offshore platforms (Unger 1966; Gooding and Magnuson 1967; Hunter and Mitchell 1967, 1968; Klima and Wickham 1971). Springer and Woodburn (1960) noted that *S. barracuda* occurred near shipwrecks off the Tampa Bay area but not on natural rocky reefs. The occurrence of barracuda may be associated with the higher relief of structures such as shipwrecks or the stages. In this respect the offshore platforms are ideal for attracting large numbers of typically open-water fishes.

Sharksuckers (remoras) were often seen associated with other fish species around the stages (especially the larger pelagic species such as *Caranx hippos* and *S. barracuda*) but were never numerous. The species was probably *Echeneis neucratoides,* although *E. naucrates* could also be expected in the area. Four *Echeneis* were also seen attached to one of two loggerhead turtles, *Caretta caretta caretta,* which were observed asleep on the bottom below Stage I. The remoras were attached to the turtle's plastron and ventral margin of the carapace and were inactive except for movements of their opercula.

TABLE 2.—Fishes recorded at Stage II off Panama City, Fla., with estimates of usual abundance and habitat occupied.

Species	Abundance[1]				Habitat[1]
	Spring (Apr.-May)	Summer-fall (June-Nov.)	Winter Dec.	Winter Feb.	
Carcharhinidae	—	few	—	—	O
Sphyrnidae:					
Sphyrna sp.	—	few	—	—	O
Dasyatidae:					
Dasyatis sp.	—	few	—	—	B
Rajidae:					
Raja eglanteria	—	few	few	—	B
Muraenidae:					
Gymnothorax nigromarginatus	few	few	few	—	B
Congridae	—	—	few	—	B
Ophichthidae:					
Mystriophis intertinctus	few	few	few	—	B
Clupeidae:					
Etrumeus teres	—	sev-com	—	—	U
Harengula pensacolae	—	sev-abun	sev-com	—	L-U
Opisthonema oglinum	sev	com	—	—	U
Sardinella anchovia	com-abun	com-abun	sev-abun	—	U
Engraulidae	—	com-abun	—	—	L-U
Ariidae:					
Arius felis	—	few-abun	—	—	B
Batrachoididae:					
Opsanus pardus	few-sev	few	few-com	—	B
Antennariidae:					
Antennarius ocellatus	few	few	few-com	—	B
Ogcocephalidae:					
Ogcocephalus radiatus	few	few	few	—	B
Syngnathidae:					
Syngnathus sp.	—	few	—	—	O
Serranidae:					
Centropristis melana	few	sev	few-sev	sev	B
Centropristis ocyurus	com	com-abun	com	com	B
Centropristis philadelphica	—	—	few	—	B
Diplectrum formosum	sev-com	few-com	sev	sev	B
Epinephelus morio	few	few	few	—	B-L
Epinephelus sp.[2]	—	few	—	—	B
Mycteroperca microlepis	few	few-sev	few-sev	—	L
Serranus subligarius	sev	sev-com	sev-com	few	B-P
Grammistidae:					
Rypticus maculatus	—	few-com	few-com	—	B-P
Priacanthidae:					
Priacanthus arenatus	—	few	—	—	B
Apogonidae:					
Apogon pseudomaculatus	few	few-com	few-sev	—	B
Pomatomidae:					
Pomatomus saltatrix	few-sev	—	few	—	O-U
Rachycentridae:					
Rachycentron canadum	—	few-sev	—	—	O-U
Echeneidae:					
Echeneis neucratoides	—	few	—	—	(3)
Carangidae:					
Caranx bartholomaei	—	few-sev	few	—	L-U
Caranx crysos	—	sev-abun	few	—	U
Caranx hippos	—	com	sev	—	O-U
Caranx ruber	—	few-com	—	—	U
Decapterus punctatus	com-abun	abun	com-abun	com	L-U
Selar crumenophthalmus	—	sev-com	—	—	L-U
Seriola dumerili	few	few-sev	sev	—	L-O-U
Seriola zonata	few	—	—	—	U
Trachurus lathami	com	com	few-abun	—	L
Lutjanidae:					
Lutjanus campechanus	—	few-sev	sev	—	L
Lutjanus griseus	—	sev	few-sev	—	L-U
Lutjanus synagris	—	few	—	—	L
Rhomboplites aurorubens	sev	sev-com	few-sev	—	L-U
Lobotidae:					
Lobotes surinamensis	—	few	—	—	U
Pomadasyidae:					
Haemulon aurolineatum	com	com-abun	few-com	few	L
Haemulon plumieri	few-sev	few-sev	few	—	L
Orthopristis chrysoptera	com	abun	few-abun	—	L
Sparidae:					
Archosargus probatocephalus	few	sev	few	—	L-U
Calamus-Pagrus	—	few	few	—	L
Diplodus holbrooki	—	few-sev	few	—	U
Lagodon rhomboides	com	sev-com	sev-com	sev	L-U
Stenotomus caprinus	—	com	—	—	B-O

TABLE 2.—Continued.

Species	Abundance[1] Spring (Apr.)	Summer-fall (July-Nov.)	Winter Dec.	Winter Jan.	Habitat[1]
Sciaenidae:					
Equetus lanceolatus	few-sev	few-com	few-com	com	B
Equetus umbrosus	sev	sev-com	few-sev	—	B
Leiostomus xanthurus	—	com	sev	—	B
Sciaenops ocellata		few	few		B
Mullidae	—	few	—	—	O
Kyphosidae:					
Kyphosus sectatrix	—	few-sev	—	—	U
Ephippidae:					
Chaetodipterus faber	sev	few-com	sev	—	L-U
Chaetodontidae:					
Chaetodon ocellatus	—	few	few	—	B
Holacanthus bermudensis	sev-com	few-com	sev-com	sev	L-U
Pomacentridae:					
Pomacentrus variabilis	sev-com	sev-com	few-sev	—	B-P
Labridae:					
Halichoeres bivittatus	few	few-com	few	—	B
Halichoeres caudalis	sev	sev-com	few-sev	sev	B
Hemipteronotus novacula	—	few	few	—	B
Lachnolaimus maximus	—	few	—	—	L
Sphyraenidae:					
Sphyraena barracuda	—	few-sev	—	—	L-O-U
Sphyraena borealis	—	sev	—	—	U
Polynemidae:					
Polydactylus octonemus	—	—	sev	—	O
Blenniidae:					
Blennius marmoreus	few	few-sev	few	—	P
Hypleurochilus geminatus	sev-com	sev-com	—	—	P
Acanthuridae:					
Acanthurus chirurgus	—	few	—	—	B-P
Scombridae:					
Euthynnus alletteratus	sev-com	sev-com	few-com	—	O
Scomber japonicus	com	com	few	—	U
Scomberomorus cavalla	—	sev	—	—	O
Stromateidae:					
Peprilus burti	few-sev	sev	—	—	U
Scorpaenidae:					
Scorpaena brasiliensis	—	few	few	—	B
Triglidae:					
Prionotus sp.	—	few	—	—	B
Bothidae:					
Paralichthys albigutta	sev	few-sev	sev	few	B
Syacium papillosum	—	few	—	—	B
Balistidae:					
Balistes capriscus	few-sev	few-com	few-sev	few	L-U
Cantherhines pullus	—	few	few	—	P
Monacanthus hispidus	—	few	sev	—	L-P
Ostraciidae:					
Lactophrys quadricornis	few	few-sev	few	—	B
Diodontidae:					
Chilomycterus schoepfi	few	few-sev	few	few	B
86 taxa	41 species	81 taxa	57 taxa	13 species	
100%	48%	94%	66%	15%	
Number of observations	3	13	4	1	
Temperature range	17°-20°C	20°-30°C	15°-19°C	13°C	

[1]Abbreviations are as follows: sev - several, com - common, abun - abundant, B - on bottom, L - lower water column, P - on pilings, O - open water around platform, U - middle to upper water column under platform.
[2]*Epinephelus* sp. - A juvenile apparently either *E. flavolimbatus* or *E. niveatus* based upon color pattern (brownish with small white spots on lateral surface and a dark saddle on caudal peduncle, Smith 1971).
[3]*Echeneis neucratoides* on *Caranx* and *Sphyraena*.

A few species recorded at the stages are typical inshore fishes which are characteristic of coastal or estuarine areas. Examples are *Orthopristis chrysoptera*, *Lagodon rhomboides*, and *Leiostomus xanthurus*. These first two species were important members of the fauna at Stage II, while *L. xanthurus* was common at times but usually remained over the surrounding open sand bottom.

Most of the species recorded at the stages are species characteristic of rocky bottom areas offshore in the Gulf of Mexico. The platforms with their supporting pilings, as well as litter and shell hash which has accumulated in the area immediately surrounding the stages, serve as artificial reef habitat for such species. Some of the important reef species are *Gymnothorax nigromarginatus*, *Mystriophis intertinctus*, *Opsanus*

TABLE 3.—Counts of fishes at two stations below Stage II off Panama City, Fla., 1-4 August 1972. (Bold numerals are estimates.)

Family and species	Time of census (CST)									
	0129-0216	0525-0604	0715-0755	1042-1133	1152-1228	1325-1405	1519-1553	1721-1800	1833-1913	2308-2342
Station 1 (bottom)										
Ophichthidae:										
Mystriophis intertinctus	0	0	0	1	0	1	(1)	0	1	0
Clupeidae:										
Harengula pensacolae	0	0	**20**	**100**	**100**	**100**	(1)	**200**	0	0
Batrachoididae:										
Opsanus pardus	1	0	0	0	0	0	(1)	0	0	1
Antennariidae:										
Antennarius ocellatus	2	0	1	1	1	2	(1)	1	2	1
Ogcocephalidae:										
Ogcocephalus radiatus	0	1	0	0	0	0	(1)	0	0	0
Serranidae:										
Centropristis ocyurus	3	8	10	20	18	14	(1)	14	10	4
Epinephelus sp.[2]	0	0	0	0	0	0	(1)	1	0	0
Mycteroperca microlepis	0	0	1	0	0	1	(1)	0	1	0
Serranus subligarius	2	4	8	8	7	12	(1)	9	4	3
Grammistidae:										
Rypticus maculatus	4	5	4	8	1	3	(1)	5	10	6
Apogonidae:										
Apogon pseudomaculatus	2	0	2	3	0	0	(1)	1	7	3
Carangidae:										
Decapterus punctatus	0	0	0	0	0	5	(1)	0	0	0
Seriola dumerili	0	5	0	0	0	0	(1)	0	0	0
Lutjanidae:										
Rhomboplites aurorubens	0	0	2	0	0	0	(1)	4	0	0
Pomadasyidae:										
Haemulon aurolineatum	0	**30**	**200**	**200**	**300**	**300**	(1)	**200**	**100**	1
Haemulon plumieri	1	1	2	3	1	1	(1)	1	1	3
Orthopristis chrysoptera	2	**100**	**100**	**200**	**30**	**200**	(1)	**40**	11	0
Sparidae:										
Lagodon rhomboides	0	0	0	0	0	0	(1)	0	2	0
Sciaenidae:										
Equetus umbrosus	6	2	2	2	3	2	(1)	0	2	3
Kyphosidae:										
Kyphosus sectatrix	0	0	0	0	0	0	(1)	2	0	0
Ephippidae:										
Chaetodipterus faber	0	1	1	0	1	0	(1)	0	1	0
Chaetodontidae:										
Holacanthus bermudensis	0	1	4	5	2	3	(1)	1	1	0
Pomacentridae:										
Pomacentrus variabilis	0	1	10	11	13	14	(1)	12	2	0
Labridae:										
Halichoeres caudalis	0	0	6	12	22	6	(1)	9	1	0
Acanthuridae:										
Acanthurus chirurgus	0	0	1	0	0	0	(1)	0	0	0
Scorpaenidae:										
Scorpaena brasiliensis	0	0	0	1	0	1	(1)	0	1	0
Balistidae:										
Balistes capriscus	1	3	5	0	7	3	(1)	4	2	3
Monacanthus hispidus	0	0	1	1	0	0	(1)	0	0	0
Diodontidae:										
Chilomycterus schoepfi	2	1	2	0	0	1	(1)	0	0	1
Station 2 (subsurface)										
Clupeidae:										
Harengula pensacolae	0	**500**	**50**	(1)	**300**	**500**	**1,000**	**200**	0	(1)
Serranidae:										
Serranus subligarius	1	2	4	(1)	3	7	3	1	1	(1)
Grammistidae:										
Rypticus maculatus	3	0	0	(1)	0	0	0	2	2	(1)
Carangidae:										
Caranx crysos	0	**50**	**30**	(1)	**30**	7	**20**	**10**	0	(1)
Caranx ruber	0	0	1	(1)	0	0	0	0	0	(1)
Decapterus punctatus	0	5	10	(1)	**20**	2	0	0	0	(1)
Sparidae:										
Diplodus holbrooki	0	0	0	(1)	0	0	1	0	0	(1)
Lagodon rhomboides	0	6	11	(1)	12	18	12	14	0	(1)
Kyphosidae:										
Kyphosus sectatrix	5	6	1	(1)	5	2	10	0	2	(1)
Blenniidae:										
Hypleurochilus geminatus	4	2	3	(1)	2	3	2	3	2	(1)
Acanthuridae:										
Acanthurus chirurgus	0	0	0	(1)	0	0	1	0	0	(1)

[1]No census made.

[2]*Epinephelus* sp. - A juvenile apparently either *E. flavolimbatus* or *E. niveatus* based upon color pattern (brownish with small white spots on lateral surface and a dark saddle on caudal peduncle (Smith 1971).

pardus, Antennarius ocellatus, Centropristis ocyurus, Diplectrum formosum, Mycteroperca microlepis, Serranus subligarius, Rypticus maculatus, Apogon pseudomaculatus, Lutjanus campechanus, L. griseus, Rhomboplites aurorubens, Haemulon aurolineatum, H. plumieri, Diplodus holbrooki, Equetus lanceolatus, E. umbrosus, Chaetodipterus faber, Chaetodon ocellatus, C. sedentarius, Holacanthus bermudensis, Chromis enchrysurus, C. scotti, Pomacentrus variabilis, Halichoeres bivittatus, H. caudalis, Blennius marmoreus, Hypleurochilus geminatus, Ioglossus calliurus, Acanthurus chirurgus, and *Balistes capriscus*. A few natural rock outcrops which support reef faunas occur in the area, especially offshore from Stage I, but these are characteristically low in relief and are quite distinct in some ways from the habitats at the stages. They do support populations of the reef species listed above (and usually larger numbers than at the stages), but usually do not attract large masses of pelagic schooling and predatory species.

A few reef species observed at the stage habitats (such as *Abudefduf saxatilis, Pomacentrus partitus, Thalassoma bifasciatum,* and *Acanthurus coeruleus*) do not normally occur on the natural rocky reefs off the northwest Florida coast, but are tropical coral reef species which may be carried into the northern Gulf of Mexico by currents (see Hastings 1972). Such species are not permanent residents of the northern gulf, but are apparently usually killed by low winter temperatures, except for possibly during mild winters.

Comparison of the Two Stages

Although the fish faunas of the two stages were quite similar (Tables 1, 2), there were a few notable differences between the species lists for the two stages which may be significant. The most numerous species at Stage II during the summer and fall were the clupeids, *Harengula pensacolae* and *Sardinella anchovia*, and rather irregularly, *Etrumeus teres* and *Opisthonema oglinum*. These fishes formed dense schools (Figures 2, 3) below the platform during daylight hours, usually also with large numbers of carangids such as *Decapterus punctatus, Selar crumenophthalmus,* and *Trachurus lathami,* and the mackerel, *Scomber japonicus*. Such schools of baitfishes were considerably less abundant at Stage I except for during the fall and early winter (especially November and December) when large numbers of *Sardinella anchovia* and *D. punctatus* were present. Most of these had disappeared by January, however.

As might be expected, typical estuarine species, such as *Orthopristis chrysoptera, Lagodon rhomboides*, and *Leiostomus xanthurus*, were rare or absent at Stage I, even though they were quite numerous at Stage II. In contrast, *Elagatis bipinnulata*, a species typical of open, pelagic waters (Hiatt and Strasburg 1960), was recorded at Stage I, but not at Stage II, although Klima and Wickham (1971) found this species to be the most common jack congregating about artificial structures near Stage II in 1969. Other pelagic species such as *Seriola dumerili* and *Sphyraena barracuda* were also more numerous at Stage I. Similarly, some benthic species, which are characteristic of the deeper water, natural reefs in the northern Gulf of Mexico and may be rare in inshore waters as shallow as 18 m, were occasionally recorded at Stage I, but not at Stage II. Examples are *Chaetodon sedentarius, Chromis enchrysurus, C. scotti, Coryphopterus punctipectophorus,* and *Ioglossus calliurus*.

The tropical coral reef species, such as *Abudefduf saxatilis, Pomacentrus partitus, Thalassoma bifasciatum, Acanthurus coeruleus,* and *Canthigaster rostrata,* were recorded only at Stage I. These tend to be shallow-water species which apparently were able to survive by settling on the pilings and cross-members near the surface at Stage I. Such species are occasionally recorded in inshore artificial reef habitats in the northeastern gulf (Caldwell and Briggs 1957; Caldwell 1959, 1963; Haburay et al. 1969, 1974; Hastings 1972) and should be expected to occur occasionally at both stages.

Winter-Summer Contrast

Seasonal changes in the faunal composition at the stages were striking in some cases. Water temperatures recorded during this study ranged from 17° to 29°C at Stage I and from 13° to 30°C at Stage II. Lowest temperatures were recorded in January at Stage I and in February at Stage II. Highest temperatures were recorded during August and September. Changes in the fish fauna were apparently correlated with temperature, since the largest percentages of species recorded (93% at Stage I; 95% at Stage II) were present during the summer and fall, while the lowest numbers were recorded during either the winter

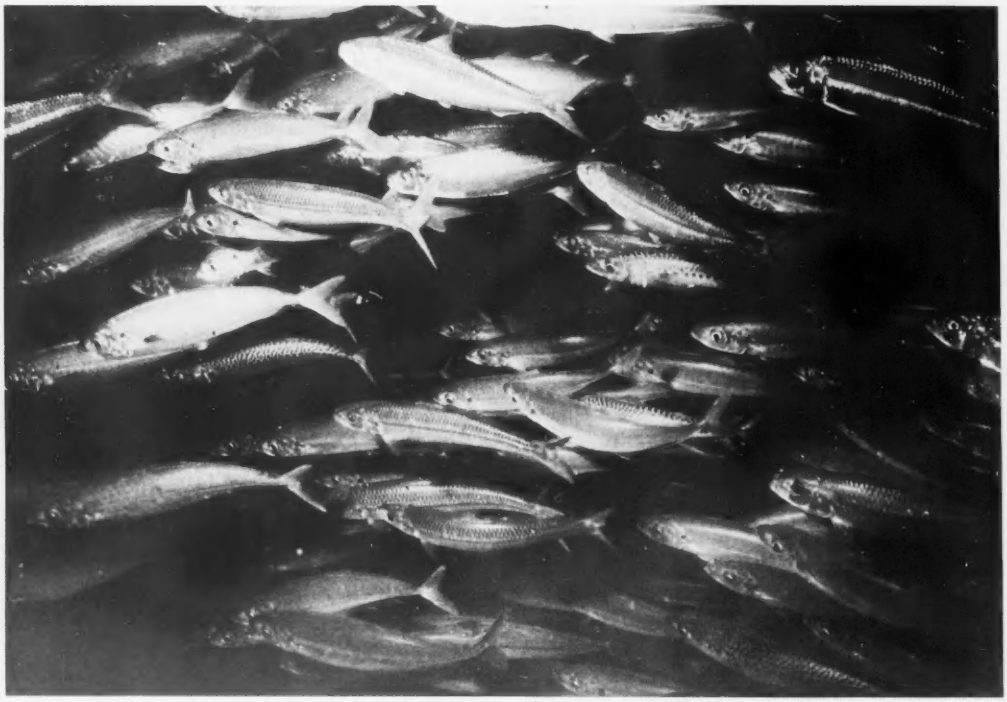

FIGURE 2.—*Sardinella anchovia, Decapterus punctatus,* and *Scomber japonicus,* in a mixed school, under Stage II off Panama City, Fla.

or spring. Estimates of abundance during the spring, summer-fall, and winter observations (Tables 1, 2) indicate that most species disappear from the area of the stages during the winter months, then gradually reappear during the spring and summer. They apparently either move offshore to deeper water, or else they migrate southward along the Florida coast (see Hastings 1972). This decrease in number of species (as well as number of individuals) occurred at both stages, but was most profound at Stage II, where temperature extremes were greater. About 50% of the number of species recorded at Stage I were present in December and January, but at Stage II, 67% were present in December and only 15% in February. These seasonal changes were most striking in the schooling clupeids and carangids (such as *H. pensacolae, Sardinella anchovia,* and *D. punctatus*) which were extremely numerous during the summer and fall, but usually rare or absent in January or February (although *Decapterus* was common at Stage II during February).

Habitat Occupation and Activity Patterns

The usual habitat occupied by each species in the vicinity of the platforms is indicated in Tables 1 and 2. Station counts for some species at Stage II, indicating diel changes in activity and occurrence at the stage, are shown in Table 3.

The pelagic species which congregate about the stages normally occupied the upper water column, either surrounding or below the platform. The clupeids, *H. pensacolae* and *S. anchovia*, formed dense schools below the platform, usually near the surface but with *Sardinella* usually somewhat deeper. The carangids, *D. punctatus* and *Trachurus lathami*, were also quite numerous, *Decapturus* normally in mid-water or near the surface and *Trachurus* very near the bottom. At times, these and other schooling species of comparable size, such as *Opisthonema oglinum* and *Scomber japonicus*, formed mixed schools under the platform (Figure 2). These species

FIGURE 3.—Large school of *Harengula pensacolae* surrounding a piling of Stage II off Panama City, Fla.

gathered in compact schools below the stage during the day apparently as a defense against predation (Hobson 1965). Station counts at Stage II for *H. pensacolae* and *D. punctatus* indicate that they left the protection of the platform and moved into the open areas surrounding the stage at night. Several species of clupeids and schooling carangids, including *H. pensacolae*, *Sardinella anchovia*, *D. punctatus*, and *Selar crumenophthalmus*, have been described as nocturnal plankton feeders (Hobson 1965; Starck and Davis 1966), although some diurnal feeding activity by *Decapterus* and *Sardinella* was observed by us and others (Klima and Wickham 1971). During daylight hours at Stage II, from about 0500 to about 1800 CST, extensive schools of *H. pensacolae* were present around and under the platform, and, at times, were so dense that they darkened the area below (Figure 3). Relatively large numbers were present at the census stations during most daylight dives, but none was observed during any of the night censuses. Similar records were obtained for *D. punctatus*, although the numbers present were considerably less than for *H. pensacolae*. In addition, *D. punctatus* may have left the vicinity of the platform earlier in the evening (about 1500 CST).

The other pelagic species are, in most cases, large predators and are continually on the move in the upper water column surrounding the platforms, occasionally darting into the schools of smaller fishes to feed. Some, such as *Seriola dumerili*, were often seen near the bottom as well. Most of these pelagic predators probably feed to some extent at night as well as during the day, and may follow the bait species, as the bait species disperse at night. However, studies indicate that many such piscivorous fishes are primarily crepuscular, with peaks of feeding activity at dawn and dusk (Hobson 1965, 1968, 1972, 1974; Starck and Davis 1966).

Only *Caranx crysos* was consistently present in the station counts (but only in Station 2 near the surface). These counts show a pattern similar to that of *H. pensacolae*, with fairly large numbers present during daylight hours and none present

at night. Possibly this jack followed the *Harengula* as they dispersed, to continue feeding through the night.

A large number of benthic reef species occupy the bottom below the platform and also the area immediately surrounding the stage, where much litter has accumulated, apparently discarded by workmen on the platform above. Other benthic species were observed on the pilings and cross-members of the platform structure, where encrusting invertebrates and algae provided food and hiding places for smaller species. In addition, habitat for benthic species may be provided by accumulations of shell hash at the bases of the pilings, probably broken loose from the pilings by storms or by the grazing of fishes or predation by other organisms. Some of the more important benthic species at the stages are *Gymnothorax nigromarginatus, Opsanus pardus, Antennarius ocellatus, Ogcocephalus radiatus, Centropristis ocyurus, Diplectrum formosum, Serranus subligarius, Rypticus maculatus, Apogon pseudomaculatus, Equetus lanceolatus, E. umbrosus, Chaetodon ocellatus, Pomacentrus variabilis, Halichoeres caudalis, Blennius marmoreus*, and *Hypleurochilus geminatus*. A few of these, such as *S. subligarius, R. maculatus*, and *P. variabilis*, seemed to be equally at home on the pilings at all levels of the water column, while others were found only near the bottom (*G. nigromarginatus, Opsanus pardus, Antennarius ocellatus, Ogcocephalus radiatus, Centropristis ocyurus, D. formosum, Apogon pseudomaculatus, E. lanceolatus, E. umbrosus*, and *Halichoeres caudalis*) or only on the pilings (*Hypleurochilus geminatus*).

An interesting contrast was noticed among members of the families Pomacentridae and Labridae at Stage I. Those species which are characteristic and permanent members of the northern gulf reef fauna (*Chromis enchrysurus, C. scotti, P. variabilis*, and *Halichoeres caudalis*) were most numerous on the bottom in association with platform supports and other objects. In contrast, species which are not permanent residents of reefs in this area, but are apparently tropical species carried north by currents (*Abudefduf saxatilis, P. partitus*, and *Thalassoma bifasciatum*) were never observed near the bottom, but were always associated with the pilings and cross-members within about 10 m of the surface. These are shallow-water species which apparently do not occur at the greater depths at Stage I (32 m).

At least two species, *G. nigromarginatus* and *Mystriophis intertinctus*, were usually seen partially buried in the substrate, often with only their heads protruding.

Several other species occurring on the bottom were most numerous over the open sandy areas surrounding the stages. *Stenotomus caprinus, Leiostomus xanthurus, Paralichthys albigutta*, and *Lactophrys quadricornis* are examples.

This benthic group includes both diurnal and nocturnal species. Species which are active and apparently feed at night are *R. maculatus, Apogon pseudomaculatus*, and *E. umbrosus*. Benthic species which are diurnal and inactive at night are *Centropristis ocyurus, D. formosum, Serranus subligarius, Chaetodon ocellatus, Pomacentrus variabilis*, and *H. caudalis*. The other species were not observed enough to determine activity patterns.

Generally counts of the nocturnal species were higher during the nocturnal observations. *Rypticus maculatus* was more numerous in Station 1 on the bottom under cross-members or other sheltering objects, but was counted in Station 2 near the surface three times, during each of the nocturnal counts between about 1730 and 0215 CST. Hiding places on the pilings are rather limited and can, in most cases, accommodate only small individuals, so apparently these soapfish were moving up the pilings at night to feed. Other references also report noctural feeding in the grammistids (Hobson 1965; Starck and Davis 1966).

Apogon pseudomaculatus, when observed at night, was active, swimming about in open areas near the bottom, while those observed during the day were always inactive, hiding among shells or other debris or under the stage cross-members. On one occasion a group of about 15 juvenile *Apogon* was seen associated with a diadematid sea urchin below a cross-member at Stage I. These small cardinal fish remained motionless among the long spines of the urchin. Cardinal fishes in general are nocturnal predators (Hobson 1965; Starck and Davis 1966; Livingston 1971).

Species of *Equetus* (or the related *Pareques*) have been reported to remain in small groups in sheltered areas by day, and then feed individually in the immediate vicinity at night (Hobson 1965; Starck and Davis 1966). Similar observations

were made during this study for *E. umbrosus*, which was present during almost every observation at Station 1.

The smaller demersal sea basses (family Serranidae) observed at the stages were relatively inactive fishes which did not exhibit obvious day-night changes in behavior. However, counts of *Centropristis ocyurus* and *S. subligarius* decreased at night, possibly indicating that some had taken shelter under objects or within shells or crevices. Literature records indicate that these and related sea basses are diurnal (Starck and Davis 1966; Bortone 1971).

Chaetodon ocellatus was usually seen swimming about near the bottom during the day and frequently in pairs. One individual observed at night resting on the bottom next to a piling exhibited the typical nocturnal color pattern described by Starck and Davis (1966).

Counts of *Pomacentrus variabilis* and *H. caudalis* at Station 1 were considerably higher during the daylight observations than at night. Daylight counts for *P. variabilis* (10-14) were less variable than those for *H. caudalis* (6-22). *Pomacentrus variabilis* is territorial and probably remains at the same general location throughout the day while *H. caudalis* is less sedentary and tends to move about more. Starck and Davis (1966) stated that *P. variabilis* and other pomacentrids are diurnal feeders which seek shelter at night in sponges, rocks, coral, or other close cover. Most of those at the stage may have taken shelter in and among the many empty mollusk shells which cover much of the bottom at the base of the stage. *Halichoeres caudalis* has not been studied previously, but several species of labrids, including *H. bivittatus* which was also present at times at Stage II, have been reported to bury themselves in sand at night (Breder 1951; Hobson 1965; Starck and Davis 1966), and this may also be the case with *H. caudalis*.

The numerous species of free-swimming fishes occupying the various levels of the water column under the platform apparently include several distinct groups based upon activity patterns and feeding habits. *Mycteroperca microlepis* is a large predator which appeared to be continually moving about under or around the stage, usually near the bottom, but a few inactive individuals were observed at night on the bottom resting against the pilings. Such species are normally described as being opportunistic feeders with peaks of feeding activity during twilight periods when the changeover of activity patterns in prey species makes them more vulnerable (Starck and Davis 1966; Collette and Talbot 1972; Hobson 1972).

Lutjanus griseus (Starck 1971), *Haemulon aurolineatum*, and *Orthopristis chrysoptera* are apparently nocturnal feeders, which utilize the stage only as a shelter during daylight hours, and move out into surrounding areas at night to feed. *Lutjanus griseus* was normally seen schooling during the day in the lower-to-middle water column under the platform. *Haemulon aurolineatum* and *O. chrysoptera* were two of the most numerous fishes in Station 1 at Stage II (Figure 4), although both were rare or absent during the nighttime observations. There may be a difference in the time of major movement for these two species. *Haemulon aurolineatum* apparently began to disperse and move out of the area at or shortly after sunset, and returned shortly after sunrise. *Orthopristis chrysoptera* possibly leaves the area under the stage earlier in the evening (just before sunset) and also may return earlier in the morning. Apparently these grunts feed at night in the open areas surrounding the stage and school under the stage as a defense against diurnal predators (Hobson 1965; Starck and Davis 1966).

Other species (such as *H. plumieri, Diplodus holbrooki, Lagodon rhomboides, Kyphosus sectatrix, Chaetodipterus faber, Holacanthus bermudensis, Acanthurus chirurgus, Balistes capriscus,* and *Monacanthus hispidus*) seemed to feed mostly on benthic organisms attached to the pilings or other objects, and may move up and down in the water column, grazing upon this material. However, some of these were more numerous near the surface (such as *D. holbrooki, L. rhomboides,* and *K. sectatrix*) while others normally remained near the bottom (such as *Haemulon plumieri, C. faber, Holacanthus bermudensis*, and *B. capriscus*). Most of these species are apparently diurnal and become inactive at night. A few *L. rhomboides, H. bermudensis,* and *B. capriscus* were observed near the bottom at night, either resting on the bottom or in protected places below cross-members or between pilings and adjacent objects. *Kyphosus sectatrix* was inactive at night, but remained in the upper water column. In contrast, *Haemulon plumieri* is nocturnal but seemed to remain in the same general area near the bottom throughout the day and night. Such

FIGURE 4.—*Haemulon aurolineatum* and *Orthopristis chrysoptera* near the bottom at Stage II off Panama City, Fla.

behavior was also noted by Starck and Davis (1966).

Starck and Davis (1966) emphasized the importance of nocturnal foraging migrations and plankton feeding to the coral reef trophic structure. Similar feeding patterns may contribute to the economy of artificial reef structures such as these offshore platforms, where abundant species of the families Clupeidae, Carangidae, Lutjanidae, and Pomadasyidae feed at night in adjacent areas, but return to the reef by day, and thus contribute to the biomass of the community.

In conclusion, the platform pilings and crossmembers, with their encrusting organisms and associated motile invertebrate fauna, provide food and shelter for numerous fish species. In addition, several diurnally schooling species are abundant beneath the platforms during the day, where they are afforded some protection from predation, but disperse into surrounding open areas at night to feed. Large numbers of piscivorous species also are attracted to the platform habitat to feed on the numerous smaller fishes associated with the structure. As the water temperature drops, many species migrate away from the platforms during the colder months. Repopulation occurs in the spring and summer.

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EFFECTS OF INCREASED WATER TEMPERATURE ON *DAPHNIA PULEX*

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ABSTRACT

Techniques were developed to study the effects of increased water temperature on certain zooplankters; specific studies were conducted on *Daphnia pulex*, an abundant and important zooplankter of the lower Columbia River. Study methods simulated prolonged exposure to constant high temperatures in thermal discharges and short exposures to increased temperatures in condensers of cooling systems. Effects were evaluated on the basis of survival and reproduction for periods ranging from 34 to 90 days. The time to death of 50% of the *D. pulex*, both mature and young, was less than 24 h at temperatures above 27°C. Temperatures of 27°C and below required an exposure of at least 192 h to cause 50% mortality. The young females were more tolerant of temperature increases than older females. The greatest reproduction by older females was at the control temperature (15°C), whereas reproduction by the young females was low at lower temperatures. No reproduction occurred above 27°C.

Two groups of *D. pulex* (one from the Seattle, Wash., area and the other from the Columbia River) studied at increased temperatures for prolonged periods revealed similar patterns of survival and reproduction, but the Columbia River group appeared less tolerant of increased temperatures. A short exposure (15 min) to increased temperatures up to 30°C had little effect on survival and reproduction.

It was concluded that temperatures should not exceed 26° or 27°C for prolonged periods or 30°C for more than 15 min to protect *D. pulex* populations in the river.

The lower reaches of the Columbia River (below Portland, Oreg.) support extensive and valuable commercial and sport fisheries as well as other types of recreational activities. This section of the river is also becoming increasingly industrialized. Associated with the industrialization is 1) the extensive use of river water for cooling purposes and 2) the discharge of heated cooling water back into the river. This increasing use of the river for industrial cooling has created concern that the aquatic biota is endangered by thermal pollution. North and Adams (1969) have described thermal conditions at outfalls and in condenser cooling systems of some California plants. They pointed out that increases of +10°F (5.6°C) above normal are considered significant biologically at all seasons of the year. Coutant (1970) presented a diagram of the hypothetical time-course of acute thermal shock to any organism entrained in condenser cooling water systems that indicates they could be exposed to the maximum increase (10.8°C) for at least 9 min in diffuser systems and to substantial increases from 12 to 20 min in the discharge canal system. He also noted the average temperature rise reported is about 10.8°C but may be as great as 16°C.

I studied the effect of increased water temperatures on one of the abundant cladocerans of the area, *Daphnia pulex*. It has been found to be important in the diet of valuable stocks of juvenile chinook salmon, *Oncorhynchus tshawytscha*, in certain seasons of the year (Craddock et al.[2]). Cladocerans may be thermally affected by a thermal nuclear power plant where, along with other zooplankton, they may be entrained with intake cooling water and pass through the condenser cooling system encountering sudden and sizable temperature increases. Increased cooling water use by industrial and power plants may increase the temperature of certain areas of the river (bays and eddies) for extended periods and also affect zooplankton.

The specific objectives of the study were: 1) to develop techniques for laboratory study of thermal effects on zooplankton and 2) to assess the

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[2]Craddock, D. R., T. A. Blahm, and W. D. Parente, 1974. Occurrence and utilization of zooplankton by juvenile chinook salmon in the lower Columbia River. Unpubl. manuscr. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash.

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effect of both prolonged and short exposure to increased temperatures on survival and reproduction of *D. pulex*.

METHODS AND MATERIALS

Two stocks of *D. pulex* were cultured at two acclimation temperatures and subjected to three types of tests to determine their thermal tolerance. One stock was obtained from the Columbia River and the other from a small pond north of Seattle, Wash. They were cultured separately and will be referred to as the Columbia group and the Seattle group. Stock cultures were maintained in 5-liter battery jars of Lake Washington water filtered through No. 25 Swiss silk bolting cloth to remove zooplankton and phytoplankton, but not bacteria. Taub and Dollar (1968) felt that bacteria were important to the nutrition of *Daphnia*, especially in relation to reproduction. Stock cultures were reared and acclimated at either 15° or 20°C in a controlled temperature incubator. Continuous fluorescent lighting (45-50 foot candles, cool white) provided similar lighting in the incubator and in the laboratory and was consistent for all animals, test and control. Algae, *Chlorella* and *Chlamydomonas*, were cultured using medium No. 63 developed by Taub and Dollar (1968) and fed to *D. pulex*. Water in the test vessels was changed weekly, and the animals were fed three times a week.

The test temperatures were maintained by using primary and secondary water baths and immersion heaters activated by temperature controllers (Figure 1). The primary bath was a Plexiglas[3] tank 150 × 30 × 23 cm supplied with flowing water at 10° to 15°C. The secondary baths consisted of six or seven 5-liter battery jars, 23 × 14 × 17 cm, placed in the primary bath. The temperature in each of these secondary baths was raised progressively from the water inlet end to the outlet end of the primary tank. Temperatures in the secondary baths could be maintained from 10° to 36°C ± 0.5°. Air continually bubbling into each secondary bath eliminated stratification. Experimental subjects were held in 50-ml jars of filtered lake water suspended in the secondary baths and equilibrated to the test temperature in those baths.

Parthenogenetically produced animals of the same age, either young females (less than 24 h old) or mature females (approximately 1 wk old), were selected from the stock cultures and held in 10-ml vials for a day before the start of the experiment to check for handling mortality. At the start of an experiment, the bulk of the water in the vials was canted off, and the appropriate number of test animals was poured directly into the 50-ml test chamber at the test temperature. The control groups were treated identically with the others, except that they were held at acclimation temperatures. A large bore pipette was used when individual animals were handled.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

FIGURE 1.—Experimental equipment used to study temperature effects on zooplankton showing primary and secondary water baths, test vessels, and temperature controllers.

Three experiments were conducted to simulate thermal conditions that *D. pulex* might encounter. Two experiments studied the effect of increased temperatures that might be encountered in the area of a heated plant outfall, whereas the third simulated the thermal conditions small organisms could encounter in the condenser cooling system of a thermal power plant.

The first experiment compared the effect of prolonged exposure (50-52 days) to constant temperatures of 15° (control), 18°, 21°, 24°, 27°, 30°, and 33°C. Test organisms were both mature females and young females (at the start of the tests) of the Seattle group acclimated at 15°C. There were 18 mature females per test temperature, 6 per test jar, and 10 young females were tested per test temperature and test jar. Ten *Daphnia* per 50-ml jar were well below the number that would cause harmful metabolic waste buildup or oxygen depletion (Pratt 1943); 10 animals has long been accepted as a standard for bioassays, Doudoroff (1951), American Public Health Association (1971), and Sprague (1973).

The second experiment compared the effect of prolonged exposure (34 days) to temperatures of 20° (control), 23°, 26°, 29°, and 32°C on mature females of the two groups (Seattle and Columbia) acclimated at 20°C. There were 10 animals per test temperature and test jar.

The third experiment subjected mature females of the Seattle group acclimated to 15°C to a short exposure (15 min) to temperatures of 15° (control), 19°, 21°, 24°, 27°, 30°, 33°, and 36°C. Test organisms were then returned to acclimation temperature where they were held and observed for 90 days. Twelve animals were tested at each temperature.

Test animals were examined frequently to determine the effect of increased temperatures, usually hourly during the first 8 h of a test. The next day or two, they were examined two or three times a day and subsequently once each week day. During each observation, the mortalities were noted and removed, and newly born *Daphnia* were counted and removed. The animals were assumed to be dead when they lay on the bottom and there was no detectable movement of the antennae, thoracic legs, or the post abdomen.

Temperature effects were evaluated on the basis of survival and reproduction by animals tested at the various temperatures. In this study, my evaluation criterion was the time at a particular temperature until 50% mortality; therefore, I use the term TD_{50} (time to death of 50% of the test animals at a particular temperature).

RESULTS

Experiments Relating to Discharges of Heated Water

Seattle *Daphnia* Acclimated to Water of 15°C

Death occurred rapidly for both mature and young *D. pulex* at 33°C. Some animals in both groups lost equilibrium within the first hour, TD_{50} occurred before the third hour, and none survived the fourth hour of exposure (Table 1). Mature and young *D. pulex* subjected to temperatures above 27°C reached TD_{50} in less than 24 h. Temperatures of 27°C and below required an exposure of at least 192 h (8 days) to cause 50% mortality. The younger females did not succumb to moderately high temperatures (18°, 21°, and 24°C) as quickly as the older females. Temperatures of 21°, 24°, and 27°C caused TD_{50} among the older females after an average of 238 h, whereas the younger females did not reach TD_{50} until an average of 768 h.

TABLE 1.—Mortality of *Daphnia pulex* introduced as mature and young females and maintained at temperatures of 15° to 33°C (Seattle race, acclimated at 15°C).

Test temp (°C)	Mature females		Young females	
	Hours to 50% mortality[1]	% mortality at end of test (50 days)	Hours to 50% mortality[1]	% mortality at end of test (52 days)
15	1,008 (42)	67	1,224 (51)	50
18	888 (37)	78	[2]1,248 (51)	40
21	259 (9)	89	1,152 (48)	60
24	192 (8)	100	648 (27)	100
27	264 (11)	100	504 (21)	100
30	19	100	21	100
33	3	100	3	100

[1]Days in parentheses.
[2]50% mortality not reached.

All animals died before producing young at 30° and 33°C; rate of reproduction was highest at 24° and 27°C before all subjects died. Total offspring produced and rate of reproduction varied for the two age-groups of females tested at 21°C or below (Table 2).

First reproduction by the mature females occurred 5 days earlier at test temperatures of 27°, 24°, and 21°C than at the control temperature (15°C). Only one peak of production occurred at 27°C before 100% mortality was reached. Reproduction at 15°C was stable with peaks occurring

TABLE 2.—Reproduction of *Daphnia pulex* introduced as mature and young females and maintained at temperatures of 15° to 33°C (acclimated at 15°C, Seattle race).

Test temp (°C)	Mature females		Young females	
	Total young produced[1]	Average no. young/adult per day[2]	Total young produced[3]	Average no. young/adult per day[2]
15	1,162	2.20	33	0.09
18	652	1.05	40	0.08
21	244	1.11	286	0.74
24	466	2.61	366	2.67
27	318	3.02	629	3.25
30	0	0.00	0	0.00
33	0	0.00	0	0.00

[1]Total reproduction from 18 animals during 50 days of experiments.
[2]Average reproduction based on number of days survivors remained.
[3]Total reproduction from 10 animals for 52 days of experiments.

regularly at 6-day intervals, whereas at higher temperatures reproduction was erratic. The greatest numbers of offspring were produced by the older females at 15°C and generally decreased with increasing temperatures. The highest rates were at 27° and 24°C where the survivors reproduced rapidly before they all succumbed on the 13th and 27th day, respectively. High temperatures increased the rate of reproduction for a short period before total mortality, but the increased rate was short lived and did not match total production by animals at a more normal temperature (15°C).

Reproduction by females who were young at the start of the experiment increased with increasing temperature, contrary to the trend shown by the older females (Table 2). No reproduction occurred at 15°C until the 34th day; at 18° and 21°C, initial reproduction took place on the 3rd to 6th day but did not resume until the 44th and 22nd day, respectively. At 24° and 27°C, the first reproduction occurred on the 3rd to 6th day, stopped for 3 or 4 days, and then continued at a high rate until the death of all females on the 34th and 27th day, respectively. The low reproduction by the younger females at 15° and 18°C is not explained.

Seattle and Columbia *Daphnia* Acclimated to Water of 20°C

Both Seattle and Columbia *Daphnia* reached TD_{50} within 24 h at 32°C (Table 3); 90% mortality occurred in less than 24 h in the Columbia group and within 48 h in the Seattle group. At 29°C, both groups reached 50% mortality in 120 h. There were significant differences in the length of time to 50% mortality for each of the two groups at 20°, 23°, 26°, and 29°C (Seattle—χ^2 = 37.9, $P<0.01$, 3 df; Columbia—χ^2 = 18.8, $P<0.01$, 3 df). The Columbia group seemed to succumb more rapidly than the Seattle group, but the more rapid demise of the Columbia *Daphnia* at 20°C (the acclimation temperature) casts doubt upon these results. However, a test of homogeneity for temperatures of 23°, 26°, and 29°C indicated significant differences between the two groups in days to 50% mortality (χ^2 = 22.6, $P<0.01$, 2 df).

TABLE 3.—Mortality of *Daphnia pulex* (Seattle and Columbia races) acclimated at 20°C and introduced as maturing females to temperatures of 20° to 32°C.

Test temp (°C)	Seattle race		Columbia race	
	Hours to 50% mortality[1]	% mortality at end of test (34 days)	Hours to 50% mortality[1]	% mortality at end of test (34 days)
20	[2]>816 (34)	40	216 (9)	70
23	648 (27)	80	456 (19)	100
26	120 (5)	100	48 (2)	100
29	120 (5)	100	120 (5)	100
32	<24 (1)	100	<24 (1)	100

[1]Days in parentheses.
[2]50% mortality not reached.

Comparatively little reproduction took place at temperatures of 26°C and above (Table 4). The greatest reproduction for the Seattle group was at 23°C and for the Columbia group at 20°C. The Columbia animals remaining after the initial unexplained mortality at 20°C outproduced the Seattle animals at the same temperature. The Seattle animals produced 62% of the total young produced by the two groups.

TABLE 4.—Reproduction of *Daphnia pulex* (Seattle and Columbia races) acclimated at 20°C and introduced as maturing females to temperatures of 20° to 32°C.

Test temp (°C)	Seattle race		Columbia race	
	Total young produced[1]	Average no. young/adult per day[2]	Total young produced[1]	Average no. young/adult per day[2]
20	246	1.12	299	1.82
23	424	1.68	152	1.02
26	0	0.00	3	0.67
29	90	2.14	16	0.32
32	0	0.00	0	0.00
Total	760		470	

[1]Total reproduction by 10 animals for 34 days of experiments.
[2]Average reproduction based on the number of days survivors remained.

Experiments Relating to Water Passing Through Cooling Systems

Exposure for 15 min at temperatures of 30°C or less seemed to have little or no effect upon the survival of *D. pulex* (Table 5). The only mortalities observed during the exposure period were at 36°C: within 5 min, over 50% of the animals at this temperature were dead; all but one died in 15

TABLE 5.—Mortality and reproduction of *Daphnia pulex* (Seattle race) exposed as maturing females for 15 min to various temperatures and returned to acclimation temperature of 15°C.

Shock temp (°C)	Survival		Reproduction	
	Hours to 50% mortality[1]	% mortality after 90 days	Total young produced[2]	Average no. young/adult per day of test[3]
15	1,178 (49)	92	2,051	3.64
19	1,320 (55)	83	1,340	2.30
21	1,008 (42)	92	1,365	3.57
24	1,512 (63)	75	2,640	3.50
27	1,464 (61)	67	1,716	2.26
30	1,536 (64)	92	1,832	2.48
33	792 (33)	100	363	0.78
36	0.083	92	[4]480	5.33

[1]Days in parentheses.
[2]Total reproduction for 90 days of test.
[3]Average daily reproduction per surviving adult.
[4]Produced by the one survivor of the 15-min exposure during the succeeding 90 days.

min. One hour after exposure, one animal had died at 33°C, but TD_{50} took 792 h (33 days) at 33°C and 1,008-1,536 h (42-64 days) after exposure to temperatures below 33°C. Time in days to reach TD_{50} was not statistically significant (χ^2 = 6.89, 5 df) for temperature treatments of 15° to 30°C. A temperature in excess of 30°C for the 15-min exposure was necessary to significantly increase mortality.

The rate of reproduction was not significantly changed by an exposure of 15 min to increased temperatures through 30°C (χ^2 = 0.79, 5 df). The greatest total reproduction was by those *D. pulex* tested at 24°C (Table 5) where survival was also good. Reproduction at 27° and 30°C exceeded the reproduction at 19°C, so it appears that reproduction is not materially affected by a short exposure to temperatures through 30°C that do not seriously affect survival. Reproduction by animals tested at 33° and 36°C was drastically reduced because most of the test animals died.

DISCUSSION

In zooplankton sampling of the Prescott-Kalama section of the Columbia River in 1968-69, *D. pulex* was more abundant during periods of higher water temperature (Craddock et al. see footnote 2). Numbers of *D. pulex* were low during the portion of the year when the temperature remained below 15°C (late fall, winter, and spring), but as water reached and exceeded this temperature the population increased rapidly until the peak abundance was reached at the maximum water temperature (approximately 21°C). The mean daily water temperature in August (the month of highest temperature) ranged from 19.3° to 22.8°C in 1968 and from 19.7° to 21.1°C in 1969 (Snyder and McConnell 1971). Tauson (1931) found temperatures of 16°-22°C favorable for parthenogenetic reproduction by *D. pulex*, but above or below this range production was reduced considerably. The upper limit was 30°C. Ivleva (1969) reviewed literature on the thermal range of *Daphnia* and noted that several researchers reported the optimum temperature range for development of *D. pulex* as 18°-20°C. Ivleva made the general observation that the optimal range varies with age and the young are more resistant to high temperature than the old, as was indicated by my experiments. Other researchers reviewed by Ivleva found that mass mortalities could occur in the range of 28°-32°C. Some of these researchers indicated that when *Daphnia* species are acclimated to higher or lower temperatures over a long period they become more resistant to further increases or reductions in temperature.

My experiments to determine the effect of increased temperature on *D. pulex* that were 1 wk old and 1 day old (i.e., at the start of the experiment) indicated that the younger animals adapted better to increased temperatures. Temperatures of 21°C and above seriously reduced the length of survival of the older females (21°C = TD_{50} in 259 h), whereas temperatures of 24° to 27°C or more were required to have the same effect on the younger females (24°C = TD_{50} in 648 h; 27°C = TD_{50} in 504 h). Temperatures above 27°C caused TD_{50} in a short time (less than 21 h) for both age-groups.

Although the younger females survived better at the control and lower test temperatures (15°, 18°, and 21°C), their eventual production of young was considerably less than that of the mature animals. This difference was not due solely to the 1-wk difference in age, and I do not have an adequate explanation.

My experiment comparing survival and reproduction of the Seattle and Columbia races indicated that the Columbia *Daphnia* may be less resistant to increased temperatures. The results of the tests of Seattle *D. pulex* acclimated at 15° and 20°C are not directly comparable and, although there is some indication that the higher temperature acclimation increases resistance in the mid-range (23°-24°C), the effect was not apparent in the high range (26°-27°C) and no conclusion could be made.

My experiments indicate that an increase of 6°C in the area of an outfall could cause TD_{50} in about 168 h (7 days) among important segments of the reproducing population. To minimize damage to *Daphnia* populations in the Columbia River, the temperature should not be raised more than 6°C above ambient or higher than 26° or 27°C for any prolonged period.

A short exposure (15 min) to increased temperatures as might occur in a condenser cooling system did not cause a significant reduction in time to TD_{50} or in reproduction unless the temperature exceeded 30°C. There is a period from mid-July through September when the lower Columbia River temperatures may exceed 20°C. In these instances, the temperature increase in condenser cooling systems should be less than 10°C if the *Daphnia* are to survive. It must be kept in mind that temperature is only one of several factors including pressure, abrasion, and toxic chemicals that could be acting synergistically to damage zooplankton in a condenser cooling system (Marcy 1973; Becker and Thatcher[4]).

To protect *D. pulex* populations, water temperatures in condenser cooling systems should not exceed 30°C and passage through the system should take less than 15 min.

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LIFE HISTORY, ECOLOGY, AND BEHAVIOR OF *LIPARIS INQUILINUS* (PISCES: CYCLOPTERIDAE) ASSOCIATED WITH THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*[1]

K. W. ABLE[2] AND J. A. MUSICK[3]

ABSTRACT

In the Mid-Atlantic Bight, spawning of *Liparis inquilinus* peaked near shore, away from sea scallop beds, in March and April. In the laboratory, females appeared to initiate spawning activity and each female probably spawned more than once. The eggs are adhesive and demersal and have been found attached to hydroids in nature. The larvae were most abundant in plankton collections inshore in May and averaged 5 mm total length at that time. Larger larvae were found in deeper water, and by 12-13 mm total length they had undergone metamorphosis and descended to the bottom where they became associated with the sea scallop, *Placopecten magellanicus*. They maintained this association from August through December. The population comprises a single year class which leaves the scallops and migrates inshore to spawn as the fish are entering their second year.

Laboratory and field observations indicated that fish were more abundant in the scallops and more scallops contained fish during the day. At night, fish left the scallops to feed on small crustaceans. *Liparis inquilinus* observed in aquaria used the fin rays of the lower lobe of the pectoral fin to detect food. These fin rays have taste buds on the surface of each ray.

Liparis inquilinus is probably protected from predation while inside sea scallops since there are few predators on the scallops of the size usually occupied. Predation while outside the scallop may be minimized by feeding only at night and then returning as soon as the fish becomes satiated. Sea scallops seem to suffer no ill effects from the association and they do not compete for food with *L. inquilinus* since *P. magellanicus* is a microplanktonic filter feeder and the former feeds on small crustaceans.

Little is known of the life history of most species of *Liparis*. Most of the meager information available for North Atlantic *Liparis* is included in Bigelow and Schroeder (1953), Andriyashev (1954), Leim and Scott (1966), and Wheeler (1969). Unfortunately, taxonomic problems remain and some published life history information may be incorrect because of misidentification. Recently, Detwyler (1963) studied the life history and reproductive biology of *L. atlanticus* from New Hampshire and Maine, and Able (in press) commented on the life history of a new species of *Liparis* from the Gulf of Maine. Elsewhere, Nizortsev et al. (1963) noted the stomach contents of *L. koefoedi*, *L. liparis*, and *L. laptevi* in the Barents Sea; Johnson (1969, 1970) reported on food habits and age and growth of *L. pulchellus* off California; Kosaka (1971) described the food habits and seasonal distribution of *L. tanakae* from Japan; Gibson (1972) mentioned the vertical distribution and feeding of *L. montagui*; and Quast (1968) described the food habits of *L. mucosus* off California.

The association between *Liparis* (= *L. inquilinus*, see Able 1973) and the sea scallop, *Placopecten magellanicus*, has been reported by several authors (Bean 1884; Goode 1884; Garman 1892; Goode and Bean 1895; Jordan and Evermann 1898; Welsh 1915; Burke 1930; Bigelow and Schroeder 1953; Leim and Scott 1966) but information is lacking on most aspects of the assocation. The purpose of this paper is to report on the life history, ecology, and behavior of *L. inquilinus*.

MATERIALS AND METHODS

The life history stages, although often overlapping, are defined as follows: larvae—planktonic individuals usually 3-13 mm total length (TL), which have not transformed to adult coloration; juveniles—sexually immature benthic individuals with adult coloration, often associated with the sea scallop, approximately 14-45 mm TL; and adults—sexually mature individuals greater than 33 mm TL. The latter can be distinguished by the presence of prickles on the body of males

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and by the enlarged abdomen of females. Scallop anatomical terminology follows Bourne (1964).

Larval *Liparis* were examined from monthly collections of the National Marine Fisheries Service (NMFS) laboratory at Sandy Hook in the Mid-Atlantic Bight during 1966-67 (Clarke et al. 1969) and from routine plankton sampling on the Woods Hole NMFS RV *Albatross IV* cruises 69-5 and 72-3 off southern New England, in the Gulf of Maine, and on Georges Bank. The larvae of *L. inquilinus* can be distinguished from those of other *Liparis* which occur in the Mid-Atlantic Bight and the Gulf of Maine by differences in pigmentation pattern in combination with size at hatching, disc formation, and notochord flexion (Able 1974). The eggs were identified on the basis of their similarity, in size of the egg and melanophore pattern of the embryo, to eggs deposited by the laboratory population of *L. inquilinus*.

Juvenile *L. inquilinus* were collected from sea scallops which were taken in otter trawls during cruises of the *Sea Breeze* while on charter to the Virginia Institute of Marine Science, and *Albatross IV* cruises 69-11 and 70-6. Other *L. inquilinus* were collected from sea scallops on *Albatross IV* cruises 68-14 and 69-8 with a 3-m scallop dredge with a 5.1-cm ring bag which was towed for 10 min at each station. On *Albatross IV* cruise 68-14, bottom substrate type and amount were estimated from the scallop dredge catch. Size and number of scallops and regular hydrographic data were also recorded. On *Albatross IV* cruise 69-8, scallop dredge tows were replicated every 2 h during a 24-h period on 4-5 August 1969. The same general area was maintained during sampling by using information from depth recorders and loran navigation. The scallop catch at each station was divided into 5-cm height classes and a representative number of scallops were examined for *L. inquilinus* from each size class.

A large series of adult *L. inquilinus* collected off the New Jersey coast in the 1930's was examined from uncatalogued material of the Academy of Natural Sciences of Philadelphia. Other small collections were obtained from a variety of sources that are too numerous to mention here.

Liparis inquilinus and sea scallops were collected between lat. 39°30′ and 40°10′N near Hudson Canyon in depths of 36-95 m and maintained in 10 to 25 gallon aerated aquaria with sand substrates for 15 mo. The aquaria were held in a cold room at 10°-11°C. Winter temperatures in aquaria dropped as low as 4°C because of the absence of heating facilities. Salinity varied from 23 to 42‰. Illumination was provided by a 60-W bulb in one corner of the room. This provided approximately 86 to 280-lx illumination for the aquaria, depending on their location in the room. The light cycle was controlled automatically and approximated that in nature. Occasional power failures caused irregular variation in photoperiod and temperature.

Liparis inquilinus were fed live amphipods, usually *Orchestia platenis* and *Gammarus mucronatus*, and the mysid shrimp *Neomysis americana* and various other small crustaceans. Sea scallops were fed a mixture of algae, *Monochrysis lutheri*, *Isochrysis galbana*, and *Phaeodactylum triconutum*, that was added to the unfiltered aquarium water.

Pectoral fins of *L. inquilinus* were sectioned and stained with Harris' hematoxylin and eosin Y following fixation in 10% Formalin.[4]

LIFE HISTORY OF *LIPARIS INQUILINUS*

In the Mid-Atlantic Bight, spawning of *L. inquilinus* occurs near shore and away from scallop beds in the winter. In the early 1930's, over 700 adult, sexually mature and maturing *L. inquilinus* were collected from mid-December through April (Figure 1) off the coast of New Jersey and Delaware. This species was found from the Brigantine Can Buoy north of Atlantic City, N.J., to near the mouth of Delaware Bay and inside the bay at Old Bare Shoal and in deep holes off Brandywine (Shoal?) and Lewes, Del. Most of the collections were in 7-14 m; however, part of this series was from depths as shallow as 3-4 m "off New England Creek (near Cape May Co.)." Unfortunately, we have been unable to locate this area in New Jersey. Recently (January-March 1971 and January-February 1973) other mature adults were found off New Jersey, especially off Little Egg Inlet in depths from 4 to 7 m. Sea scallops were never taken in the vicinity of these collections (D. Thomas pers. commun.).

The average total length of *L. inquilinus* increases from December through April (Figure 1). Detwyler (1963) attributed an increase in total

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

length of *L. atlanticus* during the winter to the replacement of smaller adults by larger adults as the spawning season progressed. This may occur for *L. inquilinus*, but it seems more likely that sexually immature fish moving inshore in November, December, and January may continue to grow as they become sexually mature. In the laboratory, fish continued to feed during spawning periods. Although the range in total length for collections for each month is large, the variation about and between the means is small (Figure 1). This probably indicates that a single year class is present in each sample.

Spawning in *L. inquilinus* probably peaks in March and April. A single collection of *L. inquilinus* eggs was made on 9 March 1973, approximately 3.5 nautical miles off Holgate, Long Beach Island, N.J. Also, the adult fish represented in Figure 1 were examined for sexual maturity. The percentage of sexually mature fish increased from 12% in January, to 44% in February, and to 67% in March, but decreased to 33% in April, although this last sample was small. Hatching times for other *Liparis* vary from 22-30 days for *L. atlanticus* (Detwyler 1963) to 6-8 wk for *L. liparis* (Breder and Rosen 1966). Therefore, the occurrence of *L. inquilinus* larvae averaging 5 mm in May (Figure 1) infers that spawning probably takes place in March and April, and this is in agreement with the time of occurrence of sexually mature adults in inshore waters.

In the laboratory, reproductive activity and egg laying occurred over many months. During 1969, females distended with eggs and performing prespawning behavior (see below) were present from January through August. Eggs with eyed larvae were first found in late April and egg masses were found through June. Successful hatching occurred only in May. The extensive period of egg deposition and reproductive behavior observed in the laboratory does not agree with the limited reproductive period inferred from field collections. These differences may be attributable to the occasional power failures which affected photoperiod, water temperature, and water quality in the laboratory aquaria or simply to laboratory confinement.

It is likely that the average size of sexually mature males and females is similar and that the sex ratio is 1:1. A single collection of 143 *L. inquilinus* (off New England Creek, 7 m, 22 February 1933) contained 75 mature and maturing males (mean 55.3 mm TL, range 37.1-69.6 mm TL) and 68 females (mean 54.3 mm TL, range 44.3-65.7 mm TL). Neither the ratio of males to females nor the average total length was significantly different.

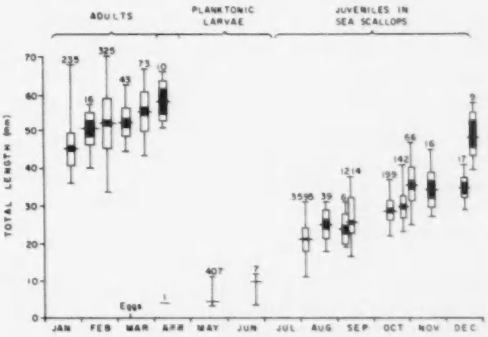

FIGURE 1.—Length-frequency distribution of *Liparis inquilinus* collected from the Mid-Atlantic Bight. For each sample, the range is represented by the vertical line, mean by the horizontal line, one standard deviation on each side of the mean by hollow rectangles and two standard errors on each side of the mean by solid rectangles. Numbers above figure are sample sizes. A single collection of *L. inquilinus* eggs is noted on the horizontal axis.

Female *L. inquilinus* may spawn more than once. In the laboratory, the abdomen of individual fish was observed to decrease in size as more egg masses were found in aquaria and increase again later. Also the egg diameters in ovaries of females from 16 March 1932 and 1933 usually had two well-defined modes. Fourteen ovaries were examined and most eggs were either 1.00-1.30 or 0.01-0.50 mm in diameter. The largest eggs were clear and contained several oil globules and these were more abundant in the center of the ovary. When egg diameter modes in the ovary were not well-defined, egg distribution by size was often random. Counts for the larger eggs ranged from 105 to 1,135 (mean 447) in seven ovaries from females raised in the laboratory and from 231 to 563 (mean 342) for females collected off New Jersey. The high count for females raised in the laboratory may have been due to the failure of the female to spawn and continued development and accumulation of the eggs in the ovary because of disturbances in the laboratory. There seemed to be no correlation between fish size and egg numbers. The average number of eggs is less than the 475 to 700 eggs reported for *L. atlanticus* (Detwyler 1963), a larger species.

Spawning Behavior

Female *L. inquilinus* may initiate spawning activity. In laboratory aquaria females with distended abdomens were the most active. They often swam in quick dashes around the sides of the aquarium then up to the surface and down again. During these dashes, the snout came out of the water and there was considerable splashing. Similar behavior has been reported for *L. atlanticus* females (Detwyler 1963). This activity often lasted several minutes and on one occasion 7 min and 20 s. Occasionally during these excited dashes the females would bump into other fish, both males and females. In a few instances, this activity seemed to excite other females and they also became active. In one instance, a ripe female repeatedly nudged with her snout a fish of unknown sex that was attached to the side of the aquarium. Soon a prominent bulge appeared just posterior to the genital papilla of the female. This has been observed just before spawning in *L. atlanticus* (Detwyler 1963) and *Cyclopterus lumpus* (Cowan 1929). In this instance, the nudged fish did not respond and the female swam away. The bulge receded after about 5 min. Sexually mature males are covered with numerous prickles while the females usually lack these or have only a few. Thus, the female may be able to recognize males by making contact with them. Breeding tubercles and contact organs in fishes may function in maintenance of body contact between the sexes during spawning and stimulation during breeding (Wiley and Collette 1970). The prickles on *L. inquilinus* males may function in these ways also. Spawning was not observed but is probably similar to that in *L. atlanticus* (Detwyler 1963). In the laboratory, *L. inquilinus* deposited small clumps of 20-80 eggs on the bottom of the aquaria and did not guard them. The eggs collected on 9 March 1973 off New Jersey were attached to hydroids as has been reported for *L. liparis* (Ehrenbaum 1905). The larvae that hatched in the laboratory did not survive beyond yolk sac absorption.

Larvae

In the Mid-Atlantic Bight, larvae of *L. inquilinus* are planktonic during the spring. During monthly larval fish surveys in 1966-67 by the Sandy Hook Laboratory, 98% of the *L. inquilinus* larvae were collected in May (Figure 1) from deep and shallow tows. These averaged 5.1 mm TL (range 3.2-12.0 mm TL). Larvae were most abundant in samples collected nearest to shore (Figure 2). Other larvae of the same average size have been collected during May from inshore waters in the Gulf of Maine and on Georges Bank (Table 1, Fig. 3). Larvae larger than 13 mm TL were usually not found in the plankton.

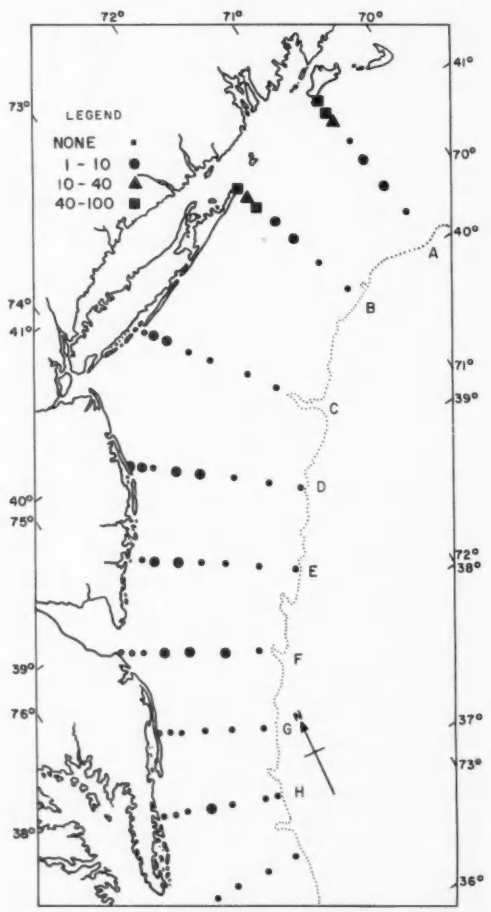

FIGURE 2.—Distribution and abundance of larval *Liparis inquilinus* from *Dolphin* cruise D-66-5 during May 1966.

Juveniles

In the Mid-Atlantic Bight, juvenile *L. inquilinus* are associated with sea scallops from August through December. Stevenson[5] reported

[5]Stevenson, J. A. Fish. Res. Board Can., St. Andrews, New Brunswick, Manuscr. Rep. 373.

TABLE 1.—Collections of larval *Liparis inquilinus* from plankton sampling cruises. Mean followed by range in parentheses.

Item	*Dolphin* 66-3	*Dolphin* 66-5	*Dolphin* 66-7	*Albatross IV* 69-5	*Albatross IV* 72-3
Locality	Mid-Atlantic Bight	Mid-Atlantic Bight	Mid-Atlantic Bight	Georges Bank	Southern New England Gulf of Maine Georges Bank
Date	8 April 1966	12-20 May 1966	18-27 June 1966	22-26 May 1969	6-16 May 1972
Water depth (m)	—	—	—	73.0(65-88)	65.8(36-96)
Number collected	1	414	7	28	73
Number measured	1	269	7	26	32
Total length (mm)	3.8	5.0(4.0-11.0)	9.4(3.4-11.5)	5.8(3.5-15.7)	4.6(3.7-10.0)

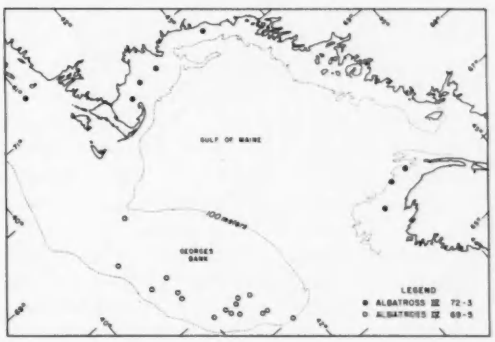

FIGURE 3.—Locations of collections of larval *Liparis inquilinus* from *Albatross IV* cruises 69-5 and 72-3.

Neoliparis (Liparis) atlanticus from sea scallops as early as July in the Bay of Fundy off Digby, Nova Scotia. Specimens we have from sea scallops in that area are all *L. inquilinus*. Juvenile *L. inquilinus* have also been collected from scallops from Georges Bank in July and may be present in sea scallops during July in the Mid-Atlantic Bight as well. The fish found in the scallops during August (Figure 1) corresponded in size with that expected from the earlier collection of planktonic larvae (Figure 1) and represented the same year class. The average total length of fish from scallops increased steadily from August through November (Figure 1). The small variation in each collection indicated that there was a single year class inhabiting sea scallops during a single year. *Liparis inquilinus* have been collected from sea scallops as late as mid-December (17 Dec. 1967, lat. 38°20′N, long. 73°59′W, 66 m and lat. 38°18′N, long. 74°23′W, 42 m) (Figure 1). The absence of fish in the scallops collected in January (18 Jan. 1968, lat. 38°34.5′N, long. 73°36′W, 62 m; 26 Jan. 1968, lat. 38°05′N, long. 74°13′W, 66 m) corresponds with the appearance of *L. inquilinus* inshore off Delaware and New Jersey during the same periods. These mature and maturing fish represent the same year class as the juveniles that were associated with sea scallops. Therefore, *L. inquilinus* reproduces when 1 yr old in the Mid-Atlantic Bight.

Adults may not survive to spawn the following year. Specimens larger than 50 mm have never been taken from May through December. The life history of *L. inquilinus* in the Mid-Atlantic Bight is summarized in Figure 4.

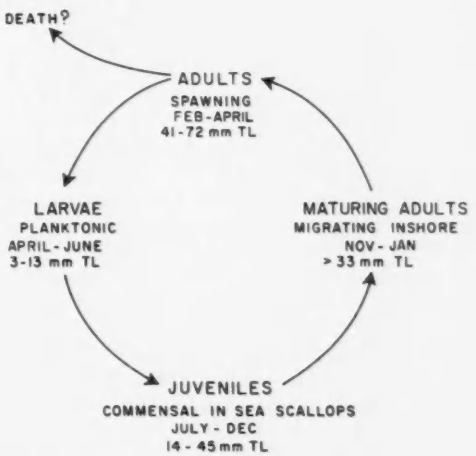

FIGURE 4.—Schematic presentation of the life history of *Liparis inquilinus* in the Mid-Atlantic Bight.

ECOLOGY AND BEHAVIOR OF *LIPARIS INQUILINUS* ASSOCIATED WITH SCALLOP

Resting

In aquaria, *L. inquilinus* preferred an inverted resting position with the disc attached to any smooth substrate such as the side of the aquarium, the interior of mollusk shells, rocks, or glass containers. Once attached, the fish flexed its

tail so that the caudal fin was alongside the head. From 13 November to 20 December 1968, observations were made on the position of fish attached to four hinged sea scallop shells or "clappers." These were positioned on the bottom of an aquarium, with one of each of these pairs placed with the right valve (flat valve) up and the left valve down. One value rested on the bottom and the other was at an angle of approximately 30°-40°. Of 40 observations, 95% of the fish in shells were attached upside-down to the top valve of the clapper with as many as eight attached to the same valve. The inverted resting position was also the most commonly observed during the remainder of the time fish were maintained in the laboratory.

Feeding

Liparis inquilinus has several morphological and behavioral adaptations which may allow it to feed at night. In aquaria, fish swimming over the bottom appeared to depend on reception of tactile and/or gustatory stimuli received by the head and pectoral fins. Swimming resulted from the combined action of the tail and the upper lobe of the pectoral fins. The eight or nine filaments in the lower lobe of the pectoral fins were extended vertically toward and often touched the bottom. When amphipods were placed in aquaria, fish did not appear to respond to visual cues but feeding usually occurred when the head or the lower lobe of the pectoral fin touched an amphipod. If food touched the head, it was immediately ingested. If food touched the pectoral fin, the fish quickly backed up or arched its body to the side and sucked in the prey. The rays in the lower lobe of the pectoral fin of *L. inquilinus* contain dark staining buds along the surface of each ray (Figure 5A) which are most abundant at the tips (Figure 5B). They are identified as taste buds on the basis of their similarity to the figures presented by Bardach and Case (1965). They described the sensitivity of the pelvic fins in *Urophycis chuss* and the pectoral fins in *Prionotus carolinus* and *P. evolans* to gustatory stimuli. Freihofer (1963) suggested that the particular pattern of the ramus lateralis accessorius nerve to the pectoral and pelvic fins in the Liparidae allows the development of these fins as "sensory, locomotor and support appendages." The well-developed cephalic lateralis system of *L. inquilinus* may also function in detecting moving prey. Occasionally fish sucked in amphipods which passed within less than 1 inch of the head.

Liparis inquilinus feeds on benthic prey. Stomachs of fish collected in nature contain almost exclusively small crustaceans and small numbers of sand grains. In the laboratory, sand from the bottom was frequently sucked in with food items and then discharged from the gill opening. A round mouth, as in *L. inquilinus*, is well-adapted to sucking in prey (Alexander 1967).

Behavior of Fish Associated with Sea Scallops

The association between *L. inquilinus* and sea scallops is well-developed and both partners show definite behavioral adaptations. Fish collected from sea scallops were isolated from them for several weeks. Upon reintroduction of fish into aquaria containing acclimated sea scallops, many of the fish swam around and over the scallops but concentrated most of their activity along the scallops' mantles. Most fish alternated between swimming parallel to the mantle with the lower lobe of the pectoral fin extended toward it or swimming with the head oriented directly toward the mantle. The tentacles on the mantle often contracted but the valves did not close. On one occasion a fish "mouthed" a tentacle, an action similar to the acclimitization behavior of some pomacentrid fishes associated with anemones (Mariscal 1966). On two occasions, fish attached to the mantle, and in one of these instances the tentacles of the scallop mantle moved over the body of the fish and depressed the anterior portion of the dorsal fin. There was no reaction by either partner and eventually the fish attempted unsuccessfully to enter the scallop.

The tentacles of the sea scallop are tactile and chemical receptors (Bourne 1964) and may be able to discriminate between *L. inquilinus* and other fishes. In aquaria, sea scallops exposed to individuals of *Gobiosoma bosci* and *Gobiesox strumosus* reacted negatively, when the mantle of the scallop was brushed by either species, by closing the valves. Similar results were observed when *Fundulus heteroclitus* and *Tautogolabrus adspersus*, were exposed to sea scallops (Musick 1969).

Liparis inquilinus occasionally may enter an alternate host species. Hoff (1968) reported a specimen of *L. atlanticus* from the bay scallop, *Aequipecten irradians*, in Buzzards Bay, Mass.

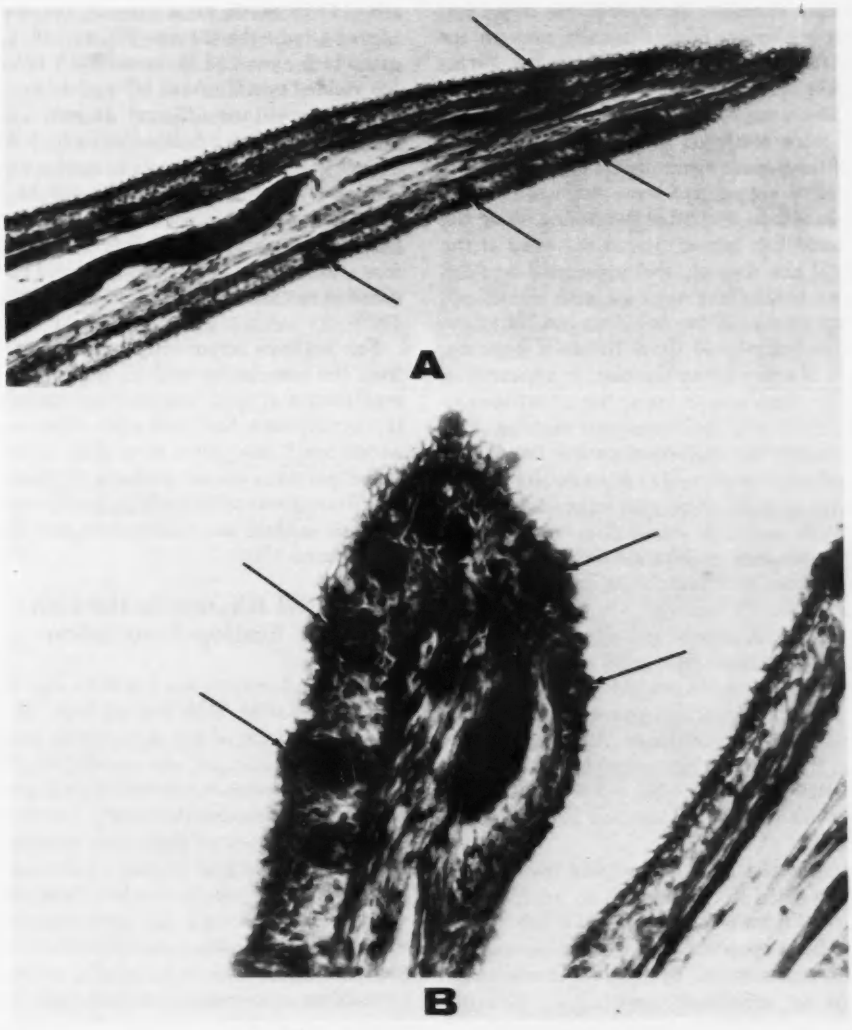

FIGURE 5.—Section through a fin ray from the lower lobe of the pectoral fin of *Liparis inquilinus* stained with hematoxylineosin. Arrows indicate taste buds. A. Taste buds on margin of fleshy portion of fin ray. B. Numerous taste buds at the tips of the fin rays.

We identified a specimen provided by him as *L. inquilinus*. Since that initial occurrence he has collected several other *Liparis*, which are probably also *L. inquilinus*, from bay scallops (pers. commun.). *Liparis inquilinus* originally collected from sea scallops were placed in aquaria with bay scallops to determine if they would attempt to enter the scallops. These scallops were completely ignored and the fish made no attempt to enter or attach to them. When brushed by *L. inquilinus*, the bay scallops either showed no response or closed the valves slightly. Bay scallops are found in much shallower water than the sea scallops, and the occurrence of *L. inquilinus* in depths frequented by bay scallops is unusual. These fish which occur in shallower water may attempt to associate with bay scallops in the absence of their regular host. Confusion in host recognition may

occur where chemical stimulation is important but other ecological factors usually prevent the animal from associating with other forms (Davenport 1955).

Over 30 attempts by *L. inquilinus* to enter sea scallops were observed in the laboratory. The length of time spent swimming along the mantle of the scallop varied, but some fish were able to enter in less than 3 s. After swimming along the mantle most fish turned, placed the head at the margins of the mantle, and attempted to force their way inside the scallop with sustained swimming strokes of the tail. One individual repeated this activity 10 times before it gave up. The point of entry along the mantle appeared to be selected randomly. Several fish attempted to enter the incurrent and excurrent opening. The scallop usually did not react to the fishes' entrance and only occasionally responded by closing the valves slightly. The red hake, *Urophycis chuss*, enters and exits the scallop only through the excurrent opening (Musick 1969).

Perhaps there is individual variation in the acceptance of fish by scallops. On two occasions, scallops rejected *L. inquilinus* after they had entered the scallop by clapping the valves together and thus forcing the fish out of the mantle cavity. In each instance, the fish came to rest a few inches from the edge of the scallop. The fish remained still as the sand stirred up by the scallop's activity settled over it. Within a few minutes, the fish returned to the scallop and attempted to enter again.

Once inside the mantle cavity of the scallop, the fish attached by their discs in an inverted position to the mantle tissue of the left valve. Fish have been observed in this position approximately 20 times, either by viewing through the excurrent or incurrent opening or picking the scallop out of the water and looking in as it clapped. Often several fish were observed in the same scallop simultaneously. This position in the scallop is the same as that preferred by fish attached to clapper shells and other smooth substrates. In approximately 100 other instances, *L. inquilinus* presence in sea scallops was confirmed by their absence elsewhere in the aquaria.

Liparis inquilinus and *U. chuss* apparently cooccur in sea scallops frequently and in considerable numbers. We have collected these fishes together in sea scallops from Georges Bank in September, November, and December. In the Mid-Atlantic Bight (4 August 1969, lat. 39°40'N, long. 73°09'W, 40 m) a 141-mm sea scallop contained a red hake (21 mm TL) and 21 *L. inquilinus* which averaged 16.5 mm TL. A 125-mm scallop yielded two *U. chuss* (43 and 47 mm TL) and two *L. inquilinus* (23 and 24 mm TL). Goode (1884) also reported *L. lineatus* (= *inquilinus*) and *Phycis* (= *Urophycis*) *chuss* as companions in sea scallops. These two fishes may not be in direct competition for this particular habitat since the *L. inquilinus* remain attached to the upper surface of the cavity and *U. chuss* swims in the middle of or rests on the bottom of the cavity (Musick 1969).

Sea scallops apparently suffer no ill effects from the association with *L. inquilinus*. Of several thousand host sea scallops opened during this study, none had noticeable internal damage which could have been caused by *L. inquilinus*. These partners do not compete for food since *L. inquilinus* feeds principally on larger crustaceans and sea scallops are microplanktonic filter feeders (Bourne 1964).

Diel Rhythm in the Fish—Scallop Association

Juvenile *L. inquilinus* exhibit a diel rhythm in their association with sea scallops. In aquaria, fish were outside of the sea scallops and actively swimming during periods of darkness. The color pattern of the fish faded during dark periods but returned within approximately 5 min after the lights were turned on. Fish were usually inside of scallops or attached to some substrate in the aquarium during light periods. When the lights went off on their regular cycle, the fish would often leave the scallops and become active within 5-10 min. These reactions to light and dark were immediate even when the dark-light cycle was changed drastically during a single day. *Liparis inquilinus* which were collected from sea scallops during a 24-h period on 4-5 August 1969 near Hudson Canyon (Figure 6) exhibited the same pattern (Figure 7). During this period, 3,595 *L. inquilinus*, averaging 21.0 mm TL, were collected from 616 of the 841 scallops examined. In one instance, 32 fish were found inside a 139-mm scallop. Fish were more abundant in scallops and more scallops contained fish during the day than at night (Table 2). However, some fish were present in scallops during every sampling period. The greatest increase and decrease in the number of fish per scallop occurred around sunrise and sun-

set respectively. The number of fish per scallop was high during the day (Figure 7) and declined substantially in the first sample after sunset. After the initial decrease in the numbers of fish per scallop after sunset, the number increased regularly up to daytime levels as sunrise approached. The number of fish in scallops was slightly greater than presented in Figure 7. Fish found outside of scallops (122 or 3% of the total) in the collecting buckets or on the deck were not included in the averages. However, these fish were more abundant at stations where the number of fish per scallop was greater so that they did not affect the comparative data.

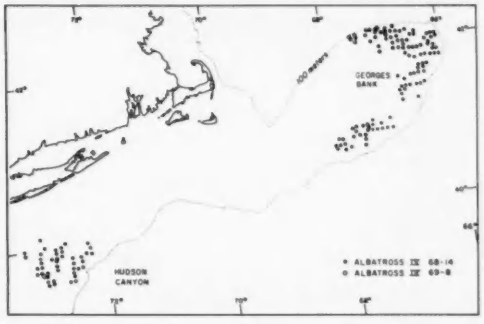

FIGURE 6.—Locations of sampling sites for fish-scallop association on 5-17 September 1968, *Albatross IV* cruise 68-14 and on 4-5 August 1969, *Albatross IV* cruise 69-8.

The majority of *L. inquilinus* leave scallops to feed during the night and then return near sunrise or as they become satiated. Sixty stomachs were examined (five from each sampling period) and were assigned a separate value for relative fullness (0-4) and state of digestion of contents (1-3) with the highest numbers given to stomachs with the most food and the least degree of digestion. When added together, these give a relative value referred to as the stomach analysis index. The maximum value possible is 7, the minimum is 1. The higher values should be from fish which had recently fed, and digestion had not begun or had not progressed very far. The stomach analysis index values increased from 2200 h, with highest values occurring just before and after sunrise (Figure 8). The lowest values were found just before and after sunset (Figure 8). Whole undigested amphipods were found in stomachs of fish taken at night, but after 0800 h stomach contents were in increasingly advanced stages of

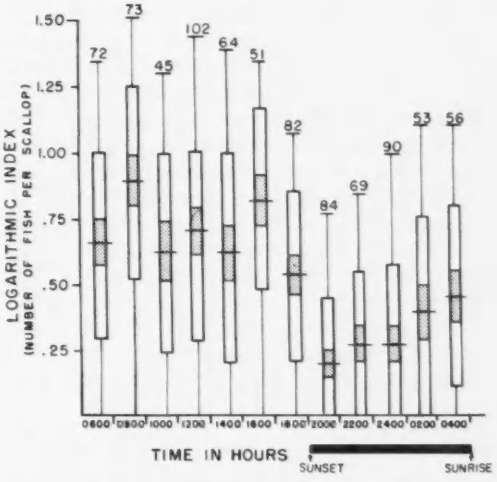

FIGURE 7.—Number of *Liparis inquilinus* per scallop from the combined total of two 10-min tows taken every 2 h over a 24-h period on 4-5 August 1969 at approximately lat. 39°39'N, long. 73°08'W. For each sample, the range is represented by the vertical line, mean by the horizontal line, one standard deviation on each side of the mean by hollow rectangles and two standard errors on each side of the mean by solid rectangles. Numbers above each figure represent the number of scallops sampled.

TABLE 2.—Comparison of the number of *Liparis inquilinus* in sea scallops during the day and night for a 24-h period.

Time	Number of scallops examined	Mean number of fish per scallop	Percent of scallops with fish	Number of replicated stations
Day (0503-1908 h)	489	6.1	86.3	7
Night (1909-0502 h)	352	1.7	57.3	5
Total	841	4.2	73.2	12

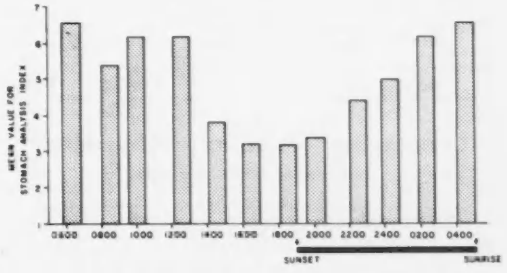

FIGURE 8.—Results of stomach analysis of *Liparis inquilinus* taken from scallops over a 24-h period on 4-5 August 1969. Stomach analysis index value for each stomach was derived from ranking relative fullness (0-4) which is added to the state of digestion of the contents (1-3), with the highest numbers given to stomachs having the most food and the least degree of digestion.

digestion until only unidentifiable material remained in stomachs collected just before and after sunset. Fish with full stomachs and undigested contents were first collected at 2200 and 2400 h. These were probably returning to scallops as they became satiated. All fish do not leave the scallops at sunset (Figure 7). Some may remain if they still have food in their stomachs. Those fish examined around 2000 h did not have completely empty stomachs (Figure 8). None of the fish examined at 0200 and 0400 h had empty stomachs.

The number of *L. inquilinus* occupying sea scallops probably decreases through the fall and early winter. During September 1968, 43 collections near Hudson Canyon (Figure 6), which overlapped the collecting area in August 1969 (Figure 6), yielded fewer fish per scallop (Table 3) than in August. These differences could be due to relative year-class strength or may reflect an actual change in the number of fish occupying scallops later in the year. Mortality of *L. inquilinus* owing to predation or a breakdown in the association as the fish grow larger could explain a decrease of this magnitude. Small numbers of sea scallops collected during the fall and early winter of several years did not yield as many *L. inquilinus* as were collected earlier in the year.

Size of individual sea scallops may be a factor in their selection by fish. In one instance, a 60-mm scallop contained a 21-mm TL fish, but it is the larger scallops which contain the largest number of fish (Figure 9).

TABLE 3.—Abundance and average total length of *Liparis inquilinus* in sea scallops from August 1969 and September 1968.

Collecting dates	Number of scallops examined	Mean number of fish per scallop	Maximum number in single scallop	Average TL of fish (mm)
4-5 Aug. 1969	841	4.2	32	21.0
14-17 Sept. 1968	717	1.7	18	26.1

Geographic Variation in Abundance of Fish in Scallops

The abundance of fish in scallops varies with geographic location (Figure 10). On *Albatross IV* cruise 68-14, 155 10-min scallop dredge tows were made as part of a sea scallop survey on Georges Bank and in the Mid-Atlantic Bight near Hudson Canyon (Figure 6). From these, 2,274 *L. inquilinus* were collected from 1,228 of the 5,905 sea scallops examined. The mean number of fish per scallop (Figure 10) and the mean number of

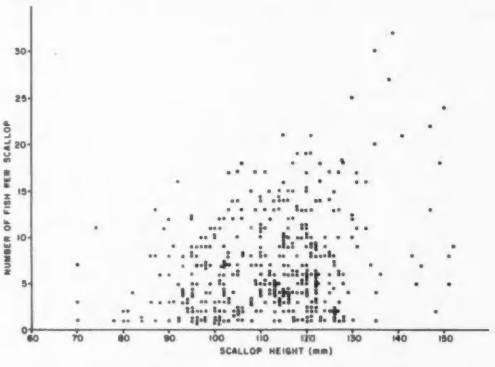

FIGURE 9.—Plot of mean number of fish per scallop versus scallop height (mm) from daytime collections from *Albatross IV* cruise 69-8.

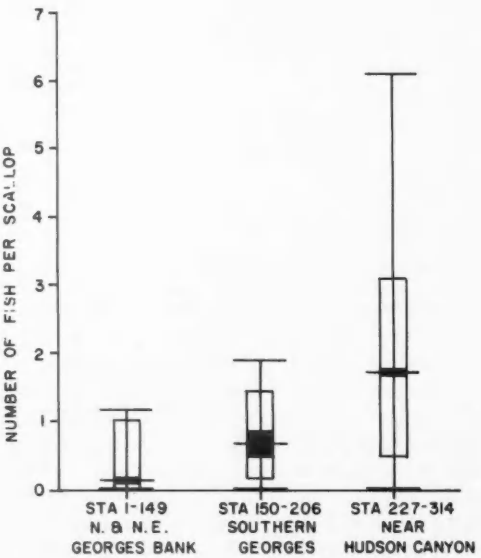

FIGURE 10.—Plot of mean number of fish per scallop at different localities from collections of 5-17 September 1968.

fish per station (Table 4) were highest north of Hudson Canyon, lowest on the north and northwest edges of Georges Bank, and intermediate on southern Georges Bank. Although the greatest abundance of fish in sea scallops occurred near Hudson Canyon, where the average depth and bottom temperature were lowest (Table 4), these parameters did not seem to be related to abundance in this area (Figures 11, 12). The average

TABLE 4.—Comparison of the possible parameters affecting *Liparis inquilinus* abundance in sea scallops over a wide geographic area. Given as mean followed by range in parentheses.

Item	Northern and northeastern Georges Bank	Southern Georges Bank	Near Hudson Canyon
No. of stations	83	29	43
Date, 1968	5-10 Sept.	10-12 Sept.	14-17 Sept.
No. of fish per scallop	0.11(0.0-1.1)	0.65(0.0-1.8)	1.74(0.0-6.1)
Scallops with fish (%)	10.1(0.0-90.9)	41.0(0.0-78.9)	59.2(0.0-100.0)
No. of fish per station	4.8(0-31)	20.6(0-64)	27.1(0-82)
TL (mm) of fish in scallops	29.4(14-47)	28.2(16-43)	26.1(17-38)
Depth (m)	77(47-95)	77(62-90)	57(37-77)
Bottom temp (°C)	10.0(4.0-14.5)	9.7(8.2-13.3)	7.8(6.5-10.1)
Clapper shells (bushels)	3.4(1-7)	5.8(2-9)	4.0(2-8)
No. scallops >60 mm per station	152(3-456)	38(10-79)	68(3-311)

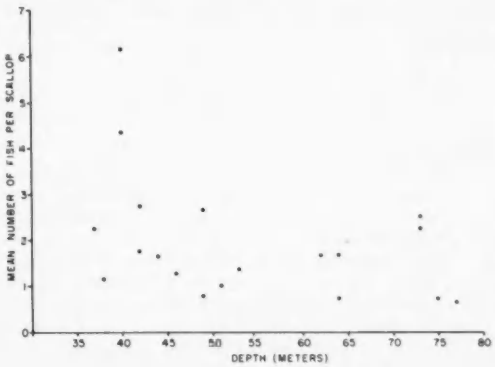

FIGURE 11.—Plot of mean number of fish per scallop versus water depth from daytime collections of 14-17 September 1968 near Hudson Canyon.

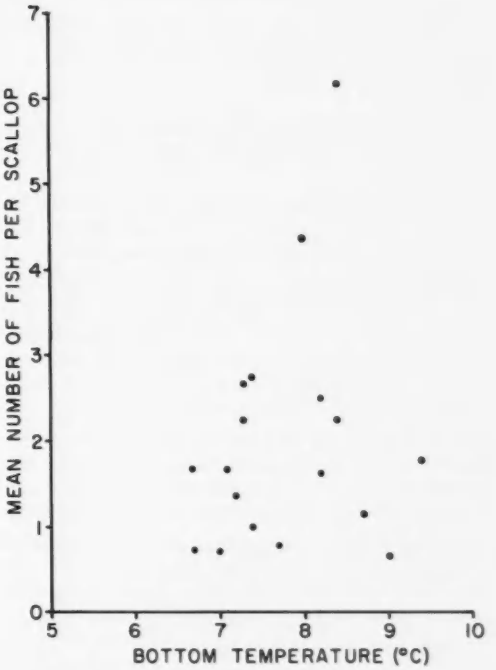

FIGURE 12.—Plot of mean number of fish per scallop versus bottom temperature from daytime collections of 14-17 September 1968 near Hudson Canyon.

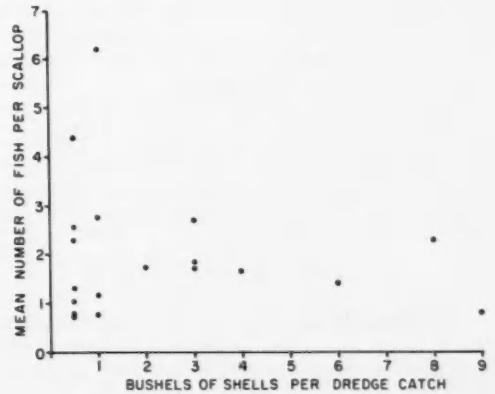

FIGURE 13.—Plot of mean number of fish per scallop from daytime collections versus clapper shell abundance from collections of 14-17 September 1968 near Hudson Canyon.

number of scallops per station for each area was not related to increased abundance of fish in scallops (Table 4). Clapper shell abundance, regardless of species, was originally hypothesized to be important in *L. inquilinus* survival and abundance since *L. inquilinus* readily occupied shells in the laboratory, and this habit may offer protection from predators. A plot of this possible relationship did not suggest a correlation (Figure 13). The similarity of abundance estimates for southern Georges Bank and the area near Hudson Canyon could be attributed to a similarity in bottom types. Both of these areas have smooth bottoms and are quite different from the rough topography of northern Georges Bank (Uchupi 1968). Fish living on smooth bottom would have less chance of concealment and evasion of predators, which would place a greater selective advantage on association with scallops. The simplest explanations for observed differences in abundance are

differences in the year-class strength and differences in actual abundance among different *L. inquilinus* populations.

Possible Advantages of the Association

Liparis inquilinus probably is protected from predation by its association with sea scallops. The only known predators of larger sea scallops which might also ingest *L. inquilinus* are Atlantic wolfish, *Anarhichas lupus*, and Atlantic cod, *Gadus morhua* (Bourne 1964). Wolfish and cod only feed occasionally on scallops and they are rare or only winter inhabitants of the Mid-Atlantic Bight. Also, *L. inquilinus* is not associated with scallops during most of the winter.

Individuals of *L. inquilinus* maximize the period of protection by associating with sea scallops for most of their demersal life. In the Mid-Atlantic Bight, *L. inquilinus* remains associated with sea scallops from the time they leave the plankton until they begin to move inshore to spawn. Also, individuals only leave sea scallops to feed and then return as soon as they become satiated. Nocturnal feeding may also decrease the possibility of detection by predators.

The relative number of scallops may not be a limiting factor for survival of juvenile *L. inquilinus*. In every sample, at any time of the year in which *L. inquilinus* have been taken with sea scallops, some scallops were always empty. However, this assumes that all sea scallops will accept fish. This remains to be proven.

The symbiosis between *L. inquilinus* and *P. magellanicus* should be referred to as a commensal association. Such an association is one in which the population of the commensal benefits and the host is unaffected (Odum 1971).

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FURTHER OBSERVATIONS OF THE FEEDING ECOLOGY OF POSTLARVAL PINFISH, *LAGODON RHOMBOIDES*, AND SPOT, *LEIOSTOMUS XANTHURUS*[1]

MARTIN A. KJELSON AND GEORGE N. JOHNSON[2]

ABSTRACT

The effect of current on feeding, temporal variation in food consumption, and the effect of predator and prey size on food preferences were evaluated for postlarval stages of pinfish, *Lagodon rhomboides* (15-19 mm total length); and spot, *Leiostomus xanthurus* (16-22 mm). Field and laboratory observations indicated that pinfish feeding rates decreased as water current velocity increased. Similar behavior was noted in spot from field observations, but spot feeding rates in the laboratory were highest when a slight current was present. Mean gut contents of postlarvae collected at midday over a 2-mo period ranged from 0.4 to 38 copepods/fish. The mean coefficient of variation for the number of copepods per fish in a single midday sample (n = 20 fish) was 20%. Maximum daily feeding rates were estimated at 17 and 26 copepods/h for spot and pinfish, respectively. Field and laboratory data confirmed that as postlarval size increases the size of their prey also increases. Refined estimates of postlarval evacuation rates and daily rations also are presented. Daily ration estimates as a percent of the fish's wet body weight were 9% for both species. The ration estimates for both species were greater than metabolic needs estimated from oxygen consumption measurements.

Information on the feeding ecology of larval fishes is necessary to understand the role of larvae in ecosystem energetics and community structure and the importance of feeding conditions to year class strength. However, relatively little is known about the feeding of larval fishes. This paper reports four major aspects of postlarval feeding: 1) the effect of current speed on feeding intensity; 2) temporal variation in postlarval food consumption; 3) the relation of feeding rate to food abundance; and 4) the effect of prey and predator size on postlarval food preferences. Refined results concerning postlarval evacuation rates and daily rations also are presented. Our earlier paper (Kjelson et al. 1975) stressed the study of food preferences, feeding intensity and periodicity, evacuation rates, daily rations, and the effect of handling and capturing the fishes on their digestive tract contents.

Pinfish, *Lagodon rhomboides*, and spot, *Leiostomus xanthurus*, constitute a major portion of the fish biomass of southeastern estuaries of the Atlantic coast and thus are important to the structure and function of these ecosystems. Spot are also an important commercial food species. Both species are primarily winter spawners in the Atlantic Ocean with larvae migrating inshore to estuarine waters which serve as nursery grounds between spring and fall. Larval forms (here defined as individuals <11 mm) are rarely found within the estuaries, whereas postlarval stages (here defined as fish between 11 and 22 mm) occur both in nearshore oceanic and estuarine waters.

METHODS

General

Postlarval pinfish (15-19 mm total length (TL)) and spot (16-22 mm) were collected during January and February 1974, from the Newport River estuary, N.C., following their recent immigration into the estuary from the offshore spawning grounds in the Atlantic Ocean. All fish were collected at Pivers Island, 2.5 km inside the Beaufort Inlet. Shore samples were collected with dip nets while those in the adjacent channel were collected with a channel net (Lewis et al. 1970). Fish were anesthetized immediately upon capture in a 0.12 g/liter seawater solution of MS-222[3] (tricaine methanesulfonate) and dissected in the

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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laboratory. Gut contents included material in the total digestive tract, from foregut to anus.

Current Speed and Feeding Intensity

Larval pinfish and spot were collected within 2 m of the shore (depth 0-2 m) where refuge from current was available and in the center of the adjacent channel (depth 5-7 m) approximately 25 m from shore where a current normally was present. Three separate collections were made for pinfish and two for spot. Twenty fish of each species from each collection were measured, dissected, and the mean number of copepods per fish determined. Surface tows for zooplankton were made at the same time and location using a 30 cm in diameter, 0.158-mm mesh net with current meter attached. Observations on copepods throughout this investigation were restricted to adult and copepodid stages. Copepod measurements were made of carapace length. Current velocities were measured with a Gurley current meter.

Feeding rates of pinfish and spot at varied current speeds also were studied in the laboratory. Fish were captured, placed in four donut-shaped, 11-liter tanks (46 cm in diameter, 10- by 10-cm cross-sectional area), and allowed to acclimate overnight in filtered, food-free seawater with no current flow. Two tanks were used as controls (zero current flow) and contained 50 and 100 fish, respectively. The other two tanks, containing 50 fish each, were attached to pumps, providing current velocities of 1.7 and 5.1 m/s, respectively. Current speed was estimated by recording the amount of time required for a minute innate particle to complete one revolution of the donut-shaped tank. At the beginning of each experiment, current flow was started in the two test chambers and *Artemia salina* nauplii (1.0/ml) were provided to each of the four tanks. Fish were allowed to feed for 1 h with additional food provided after 30 min to assume a minimum density of 1 *Artemia*/ml throughout the experiment. Twenty fish were sampled from each tank to calculate the mean number of *Artemia* consumed.

Temporal Variation in Midday Feeding

Day-to-day variation in the feeding intensity of larval pinfish and spot was studied at midday (1100-1300 h) when larval digestive tracts contained the greatest amounts of food. Fifteen collections were made from 21 January to 28 February at one site within 2 m of the shore. Each collection consisted of 20 fish of each species. Total lengths of the fish were measured, the total number of copepods in each gut counted, and a geometric mean of the number of copepods per fish calculated. Geometric means were used as a measure of central tendency because frequency distributions of the copepods or *Artemia* nauplii per fish showed a positive skewness. In addition, a geometric mean was used to limit the bias of a few individuals feeding at a rate not representative of the population because variation increased as the mean values increased.

A zooplankton tow was taken at the time and location of fish capture. The tows were made just below the surface, against the current, and sampled approximately 5 m^3 of water. Estimates of copepod density were made from three 10-ml subsamples of each tow. Twenty copepods per sample were measured for length frequencies.

Evacuation Rates

To refine our information on larval evacuation rates of copepods, two laboratory experiments were performed using pinfish and spot that had been fed an abundance of natural copepods. Four to five hundred fish were starved for 8 to 12 h and then they were allowed to feed for 1 h. Food densities averaged 2.5 copepods/ml for pinfish and 3.0 copepods/ml for spot. Larvae were acclimated and experiments run at ambient estuarine temperatures and salinities. Temperature was 12°C for the pinfish evacuation and 17°C for spot; salinity was 30‰. Following feeding, 30 fish were removed, anesthetized with MS-222 to prevent any possible regurgitation, dissected, and counts made of the numbers of copepods per fish. At the same time, three groups of 100 fish were transferred to separate food-free tanks, and the decrease in their gut contents observed by sampling 10 fish from each tank at 2-h intervals until more than one-half of the fish had empty tracts. Instantaneous evacuation rates were then calculated according to the method of Peters and Kjelson (1975). The amount of food remaining in the stomach at any time can be predicted from the following equation:

$$\log C = \log A + Bt$$

where C = content of gastrointestinal tract + 1

A = amount ingested + 1
B = evacuation rate constant
t = time.

By adding 1 to the amount ingested and to gut contents we were able to include empty gastrointestinal tracts in our calculations. From the above equation, with log base 10:

$$C = e^{2.303\,(\log A + Bt)}$$

and the instantaneous evacuation rate

$$\frac{dC}{dt} = 2.303\,Be^{2.303\,(\log A + Bt)}$$

or

$$\frac{dC}{dt} = 2.303\,BC.$$

Feeding Periodicity

Diel periodicity of digestive tract contents indicated the intensity and chronology of feeding by the fish. Our purpose was to refine the feeding chronology curve (Kjelson et al. 1975) by taking samples more frequently than in our previous study. Ten fish of each species were collected at 2-h intervals between 0600 and 1800 and at 2100 and 2400 h. Fewer samples were taken at night because our past observations have shown that larval fish cease feeding during darkness. All fish were measured, the copepods they contained counted, and a geometric mean for copepods per fish calculated for each sample.

Daily Rations

One objective of this research was to re-estimate the daily ration of larval fish for comparison with our earlier study. Daily rations were calculated by the same technique (Kjelson et al. 1975) using new information on diel periodicity of gut contents and refined measurements of instantaneous evacuation rates. Our method of calculating daily ration accounts for changes in evacuation rate which accompany diel changes in feeding intensity.

To calculate daily ration, we first estimated the average evacuation rates (in copepods per hour) for each of the 2-, 3-, or 6-h sampling periods in our feeding chronology study. This average rate was the geometric mean of the instantaneous evacuation rates at the beginning and end of each period. The estimate of food evacuated during any period is equal to the number of hours in the period multiplied by the respective average hourly evacuation rate. The total food evacuated per day was computed by summing the nine respective evacuation estimates, and is an estimate of the daily ration because the average ingestion rate must equal the rate at which material in the gut is assimilated or defecated.

Daily rations were calculated initially as copepods per fish per day and then transformed to percent of the larval body weight and calories per fish per day. Dry weights of ingested copepods were estimated from the length-weight relationship: $W = 6.274L - 0.153$ where W is the dry weight in micrograms and L is the copepod length in millimeters, based upon Heinle's (1966) data for all stages of *Acartia tonsa*. Copepod dry weights were converted to wet weights using a factor of 9.1 based upon our measurements of the wet-dry ratio for zooplankton and were compared with wet weights of the fish to compute the daily ration as a percent of live body weight. Daily caloric intake was computed using our estimation of 0.555 cal/mg wet weight of an average size copepod, based on micro-bomb calorimeter measurements of mixed estuarine zooplankton (Thayer et al. 1974).

RESULTS AND DISCUSSION

Effects of Current Speed on Feeding Intensity

Pinfish and spot larvae collected along the shore had more copepods present in their digestive tracts than those collected in midchannel (Table 1). Previous observations (Kjelson et al. 1975) indicated that neither pinfish nor spot regurgitate or defecate food under the stress of capture or handling. Thus, differences in collecting techniques

TABLE 1. — Digestive tract contents of larval fishes collected at midday at midchannel and shore stations in the Newport River estuary, January to February 1974.

Date	Species	Mean number of copepods/fish ± 1 SE		Current speed (m/s) in channel[1]	Tidal stage[2]
		Shore	Channel		
29 Jan.	Pinfish	9.1 ± 1.6	0.8 ± 0.2	1.4	LF
30 Jan.	Pinfish	19.6 ± 2.8	4.1± 0.8	0.0	HS
14 Feb.	Pinfish	20.0 ± 2.8	1.8 ± 0.6	3.2	LF
14 Feb.	Spot	14.4 ± 1.7	0.9 ± 0.4	3.2	LF
21 Feb.	Spot	2.7 ± 0.6	0.3 ± 0.2	5.5	ME

[1]No current was observed along the shore on any sample date.
[2]LF = late flood, ME = mid ebb, HS = high slack.

(channel net versus dip net) between areas were not felt to bias the results. We observed no differences in the length of fish sampled (by species) or in the density of copepods at the two locations.

These results indicate that larval feeding rates are limited when the fish are exposed to current. Current speed ranged from 0 to 5.5 m/s in midchannel where feeding was low, to no measurable current along the shore where more feeding occurred (Table 1). In addition, pinfish collected in the channel on a slack tide contained 4.1 copepods/fish compared with a mean of 1.3 copepods/fish when there was a current present.

Laboratory experiments indicated that current speed affected the food consumption rate of both species (Table 2). Pinfish consumed the most food when there was no current, but spot ate more at a current velocity of 1.7 m/s. Pinfish ate the least food in a 5.1 m/s current while the spot minimum feeding occurred at varied current speeds. Both species fed at a higher rate when fish densities were lower.

The observations from both field and laboratory studies indicate that postlarval pinfish feeding declines as current speed increases. These results suggest that current speed influences the ability of pinfish to capture their prey, although the specific reasons for such altered behavior are unknown. The well-known attack behavior of larval fish, that of visually sighting the prey and of assuming an S-shape prior to striking (Blaxter and Holliday 1963), may be unattainable by postlarval pinfish exposed to higher current speeds. Bishai (1959) found that larval herring drift with a current at speeds less than the current itself. This may suggest that the size, shape, and behavior of a plankter may influence its rate of movement in a current. Prey organisms may move at a faster rate than the fish larvae, which in turn may lessen the ability of the fish to orient to the prey.

Current also may destroy the microstructure of the prey population. Without a strong current, food could aggregate in patches thus producing local areas with high food density and therefore increase the rate of ingestion. This latter explanation is probable in the natural environment; however, it appears unlikely under the laboratory conditions, because the density of *Artemia* in the tanks was very high (1/ml) and prey were replenished to assure that it did not decrease. In addition, the small cross-sectional area (100 cm^2) and volume of the tanks greatly limited the distance a larva had to travel to find food even if prey were in a patch configuration.

Differences in channel versus shoreline feeding by spot in the natural environment (Table 1) are similar to those of pinfish; however, feeding by spot in the laboratory was highly variable and is difficult to explain. Spot fed at the highest rates when a slight current was present and even fed at a high rate when exposed to a maximum current of 5.1 m/s. The spot postlarvae used in the studies were larger than the pinfish and this may explain the ability of spot to feed at a high rate when exposed to current, because increased size usually improves swimming ability which may improve the fish's ability to capture their prey. However, species differences in swimming ability were not apparent: larvae of both species moved freely about the tank when current was absent; oriented into the current or at times drifted with the current at the 1.7 m/s speed; and drifted along with the current in the 5.1 m/s current, although some individuals oriented into the current briefly. Similar behavior by larval fishes exposed to varied current velocities was discussed by Bishai (1959) and Houde (1969). Ryland (1963) indicated that the mechanisms by which larval fishes orient to a current are poorly understood. The lower feeding rate of spot in no current is unexplainable unless this species is adapted in some way to be more effective at capturing prey within a current. Serebrov (1973) also found differences in the feeding intensity of various species (guppy, *Poecilia reticulata,* and European dace, *Phoxinus phoxinus)* when exposed to different current velocities and suggested that the differences were due both to natural adaptation to certain current condi-

TABLE 2.—Digestive tract contents (mean number of *Artemia* nauplii/larva ± 1 SE) of larval fishes following feeding in the laboratory under several current velocities.

Date 1974	Species	Length of fish (mm)	Current velocity			
			[1]5.1 m/s	[1]1.7 m/s	No current[1]	No current[2]
26 Feb.	Pinfish	16-17	2.5 ± 1.8	22.1 ± 3.5	50.9 ± 6.3	35.0 ± 4.0
3 Mar.	Spot	20-22	104.7 ± 7.5	166.0 ± 8.0	72.1 ± 7.7	23.5 ± 5.3
14 Mar.	Spot	19-20	30.3 ± 3.3	90.0 ± 5.5	39.1 ± 4.3	23.1 ± 3.2

[1]Fifty fish.
[2]One hundred fish.

tions and to the stimulation of food grasping activity caused by the increased movement of food in a current.

The highly variable nature of spot feeding in the laboratory also may be explained by the varied current conditions within the tank itself, although conditions were kept as constant as possible during the two studies. Current flow may not have been uniform throughout the tank, although the importance of this factor upon feeding is unknown. The larvae in all experiments were distributed throughout the tank and did not appear to be feeding at specific locations. The low variability in feeding rate between individual fish in each experiment, as shown by the standard errors (Table 2), suggests that all individuals were feeding at a similar rate even though they were dispersed throughout the tank. The distribution of flow across the tank vertically was not measured, although such information would be useful (Ryland 1963). The two treatment groups of spot postlarvae were from separate field collections which may have altered their behavioral characteristics sufficiently to produce the variable results.

Finally, the apparent necessity for low current velocity for feeding to take place may restrict considerably the amount of area suitable for feeding to be successful. This may be particularly true along the channels linking the oceanic habitat to that of the estuarine marsh system where our observations took place. The amount of protected shoreline and bottom habitat characterized by low current velocity along these channels is very limited compared to that present in the broad reaches of the estuary where cordgrass (*Spartina*) marsh shoreline and eelgrass (*Zostera*) beds are extensive.

Temporal Variation in Food Consumption

Considerable day-to-day variation was observed in the mean number of copepods in the plankton and in the larval fish collected at midday (Figure 1). Mean pinfish gut contents ranged from 0.4 to 38 copepods/fish while spot contained from 0.5 to 24 copepods/fish. The coefficient of variation for the number of copepods per fish in single field samples averaged 20% (range 7-40%) for pinfish, and 17% (range 8-40%) for spot. The greatest variability occurred when the average gut contents were low. Copepod density also fluctuated widely from 477 to 3,262 copepods/m³. These densities are not dissimilar from those observed during the same months in the open waters of the Newport River estuary (Thayer et al. 1974). The coefficient of variation of the copepod counts from five tows at the site of larval collections was 24%. Such variation is not high for field sampling and although it represents the variability for only a single sampling date, it does suggest that the precision of the estimate of copepod density is acceptable.

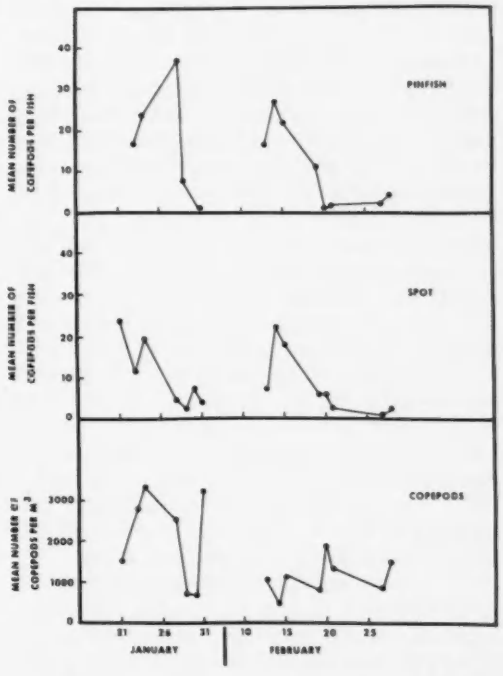

FIGURE 1. — Variation in the numbers of copepods per larval pinfish and spot, and copepods per cubic meter based on midday samples in the Newport River estuary during January and February 1974.

One of our goals was to determine if the amount of food present in larvae was related to copepod density. In our study, the correlation coefficients between copepod concentration and gut contents were very low ($r = +0.08$ for both pinfish and spot), indicating that there was no relationship. Other studies on larval fish populations have shown that feeding incidence may be correlated with food concentration (Berner 1959; Nakai et al. 1966; Bainbridge and Forsyth 1971), while Houde (1967) found no correlation between copepod abundance and feeding rate by larval walleye.

The number of factors influencing larval feeding

rates in an estuary are undoubtedly numerous; therefore, it may be difficult through field measurements to establish a relationship between larval feeding rates and food abundance. For example, the clumped distribution typical of zooplankton populations may affect larval feeding rates, with feeding limited primarily to those periods when the fish are exposed to a dense patch of copepods.

Comparing naturally occurring mean food densities with mean gut contents, to establish a relationship between prey abundance and feeding rate, presents problems if the zooplankton populations are not randomly distributed or if the fish collected were not feeding upon the same prey community sampled by the plankton net (O'Brien and Vinyard 1974). Furthermore, the aggregation of zooplankton discussed earlier may be important in determining the rate of food consumption (Schumann 1965). Ivlev (1961) indicates that patchiness in the distribution of the food material increases the ration by comparison with an even food distribution when the average concentration is the same in both cases. High consumption rates by postlarval pinfish and spot may be possible only when patches of copepods come within the feeding range of the larvae. This hypothesis is discussed by Murphy (1961). The above remarks emphasize that laboratory investigations may be required in understanding the relationships between feeding rates and food abundance.

Size Related Food Preferences

Various investigators have observed selective feeding by larval fish and, at times, definite preference for a specific food form is indicated. Much of the selectivity, however, is due to the size relationship of the larval fish and the available zooplankton (Marak 1960). Information gained from our midday field samples and our laboratory evacuation experiments enabled us to observe the relationship between fish size and the size of prey they consumed. The Wilcoxon test for paired values (Alder and Roessler 1964) was used to determine if the mean size of copepods consumed was significantly different ($\alpha = 0.05$) from those collected in the plankton tows or provided in aquaria.

The spot collected for both field and laboratory studies were significantly larger than the pinfish. Both field and laboratory results indicated that pinfish larvae always ate smaller copepods than the mean size available to them while the reverse was true for spot (Table 3). Each species consumed prey that were proportional to their size with the ratio of the mean copepod length to the average fish length approximately 1:35 based upon laboratory measurements to 1:30 based upon field data.

The above results suggest that, as the larval fish size increases, the size of the consumed prey also increases. Many researchers (Blaxter and Holliday 1963; Blaxter 1965; Ciechomski 1967; Detwyler and Houde 1970; de Mendiola 1974; Marak 1974) also have observed this relationship in a variety of larval fishes. However, the mean size consumed in each study by either pinfish or spot varied considerably (Table 3). Pinfish of similar mean sizes (16 and 16.4 mm) fed upon 590-μm copepods in the laboratory, but the 460-μm prey in the field. This difference in prey size may be explained by the apparent difference in the prey sizes available to the fish in the two studies; laboratory prey had a mean size of 663 μm while those in the field were only 515 μm. Spot size preferences, on the other hand, are difficult to explain in the same manner, because spot consumed larger prey in the laboratory than in the field, although the prey available in the laboratory were considerably smaller than those present in natural waters (Table 3).

TABLE 3.— Mean sizes of copepods eaten by larval pinfish and spot in the field and laboratory compared to the mean sizes of copepods present.

Species	Mean length of		
	Larvae (mm)	Copepods eaten (μm ± 1 SE)	Copepods in aquaria or net tow (μm ± 1 SE)
Laboratory:			
Pinfish	16.0	590 ± 29	663 ± 28
Spot	17.7	669 ± 31	491 ± 68
Field:			
Pinfish	16.4	460 ± 12	515 ± 22
Spot	20.4	581 ± 12	515 ± 22

Comparisons of mean size prey from plankton tows to those from gut contents may be difficult again due to distributional dissimilarities of both predator and prey populations during feeding and prey aggregation patterns (Schumann 1965; O'Brien and Vinyard 1974). However, these problems were lessened in laboratory aquaria where we were able to control the size, density, and distribution of the predator-prey populations.

Two primary factors appear to explain the increase in prey size as larval fish size increases.

First, mouth size usually increases as the length of larvae increases. This relationship has been documented for larval fish of various species by Marak (1960), Blaxter (1965), Ciechomski (1967), Detwyler and Houde (1970), and Shiroto (1970). A few body measurements of pinfish and spot postlarvae showed that the gape of the mouth increased as the size of the fish increased. Pinfish of 16 mm TL were estimated to have a mouth gape of 1.43 mm, while spot of 1.6 mm had a gape of 1.70 mm. The larger gape in spot may explain, in part, their consumption of larger prey. Secondly, swimming speed also increases with an increase in the fish's body size (Houde 1969; Hoagman 1974); hence, the large spot may be capable of capturing larger copepods.

Although this study emphasized the food size preferences of postlarval pinfish and spot, a topic of potential importance in the selective nature of larval fish feeding deals with the selection of specific species of copepods. We did not compare the copepod taxa in the digestive tracts with those found in the plankton tows, but such effort should provide valuable information, because copepod species differences in swimming speed, vertical position in the water, and aggregation behavior may be very important in determining the type of prey available to and finally consumed by larval fish. However, the dominant genera present in the estuary during the study period were *Centropages, Temora, Acartia,* and *Eurterpina,* common forms in the Beaufort area during winter and early spring (Thayer et al. 1974). Marak (1960) and Ciechomski (1967) attempted to assess the selectivity of larval fish for individual species of copepods, but did not observe any such preferences.

The size differences in spot and pinfish that we observed in the Newport River estuary may be due either to dissimilar spawning times, different growth rates, or both. Observations made in another North Carolina estuary (the White Oak River estuary) during 1969 indicated that estuarine spot and pinfish larval populations during January and February differed in size and that spot were significantly larger than pinfish (R. M. Lewis, pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.); spot average 18.0 mm in length while pinfish were 15.5 mm. Thus, there appears to be consistancy in the size differences observed in these two species during their influx into North Carolina estuarine waters.

Evacuation Rates

Regression coefficients for the equations describing the evacuation of copepods by larval pinfish and spot are shown in Table 4. The coefficients differ significantly from those calculated earlier (Kjelson et al. 1975). Copepod evacuation in our previous study was determined using fish collected in the estuary, placing them in a food-free environment, and observing evacuation. Those fish contained limited amounts of food at the beginning of the experiments apparently due to a low rate of feeding just prior to capture. Also, there was a 2°C difference between estuarine and laboratory water temperatures, and this may have altered the evacuation rates.

In an effort to measure the evacuation through a wide range of gut quantities and thus, hopefully, achieve a better description of evacuation, our present study used fish that initially had their guts full of copepods (21-57 copepods/fish) as determined from sacrificing 20 fish of each species at the beginning of the experiment. In addition, the possible stress of transport and rapid temperature changes in the earlier study were eliminated by using fish that had been acclimated to laboratory temperatures and that were fed in the laboratory.

The regression coefficients (slopes) achieved from our present study (Table 4) were significantly different from and approximately twice those found during the 1972-73 evacuation experiments. We consider the estimates of evacuation rates in the present study to be more representative of natural evacuation because the techniques used in measuring evacuation were more refined than in the earlier study.

The experimental temperatures, although different for the two species, were within the normal range for larvae immigrating into North Carolina estuaries. The larger negative slope in the regression model for spot compared with that for pinfish (Table 4) is probably due in part to the temperature differences (12°C for pinfish and

TABLE 4.—Linear regressions describing evacuation of copepods in pinfish and spot larvae. $Y = A + Bt$ where $Y = \log_{10}(1 + \text{mean number of copepods per larva})$ and t = hours since feeding. n = number of data points.

Species	Size range (mm)	Temperature (°C)	A	B	n	r^2
Pinfish	15-18	12	1.30	−0.18	5	0.98*
Spot	16-20	17	1.84	−0.24	5	0.98*

*$P < 0.01$

17°C for spot), because Peters et al. (1974) showed that evacuation rate of juvenile pinfish and spot is related directly to temperature.

Feeding Periodicity and Feeding Rate

Observations of larval gut contents through 24 h again indicated that these larval fish contained the greatest amount of food during daylight hours (Figure 2). Peaks in gut contents for both pinfish and spot were at 1200 h. Water temperature was 15°C.

The periodicity observed in the gut contents does not represent the actual feeding periodicity. However, if our evacuation data and model are appropriate, the feeding periodicity may be calculated from the periodicity of gut contents. Gut contents at the beginning and end of each sampling interval (Figure 2) differ by an amount equal to the amount consumed minus the amount evacuated during that time period (Peters and Kjelson 1975). Thus, we can add the amount evacuated in each interval from the change in gut content to achieve the amount ingested during the interval. Maximum hourly feeding rates (from the 1000-1200-h sampling interval) were 26 copepods/h for pinfish and 17 copepods/h for spot.

Daily Rations

Estimates of daily ration for pinfish and spot larvae were higher than those obtained from the 1972-73 study. During our earlier study, pinfish ate 38 copepods/day while the present estimate indicates 92. Previous estimates for spot were 47 and 99 copepods/day while our present estimate is 115 (Table 5). The increased ration sizes are attributed to the use of higher instantaeous evacuation rates, and in the case of pinfish, to the presence of greater amounts of food during the feeding periodicity study (Figure 2). Pinfish digestive tracts had an average of 47 copepods/fish at 1200 h during the 1974 sample day whereas during 1972 they only had 10 copepods/fish. Spot gut contents at 1200 h averaged 17, 37, and 27, respectively in the three successive years of the study.

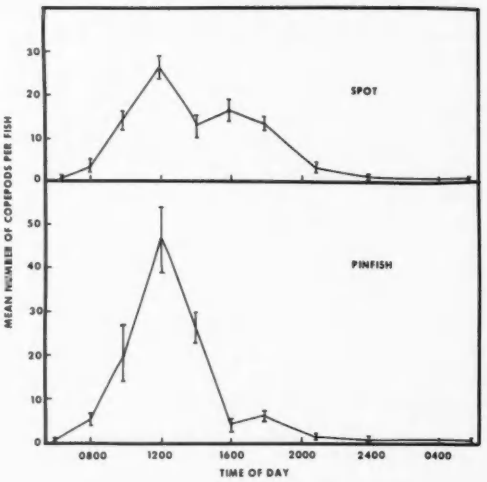

FIGURE 2. — Diel cycle of digestive tract contents in larval pinfish and spot at 15°C based upon the geometric mean of the number of copepods per fish (n = 10 fish per sampling time). Vertical bars are equal to two standard errors.

Based on our daily ration estimates of 1.3 and 2.0 cal/fish per day (Table 5) and the mean weights of the larvae, this was equal to a consumption rate of approximately 0.05 cal/mg fish wet weight per day for both species. The similarity is interesting since the average pinfish weight was only 60% that of spot and suggests that larvae of dissimilar species and sizes have similar consumption on a unit weight basis. Oxygen consumption measurements by D. E. Hoss (pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.) indicate that similar respiration

TABLE 5.—Daily rations calculated from feeding studies and O_2 consumption measurements at 15°C for larval pinfish and spot in the Newport River estuary, N.C.

Species	Mean larvae wet wt (mg)	Number copepods/ fish · day	Calories/ fish · day	Calories/fish · day from O_2 consumption[1]	
				Gilson respirometer[2]	Flowing water respirometer[3]
Pinfish	25	92	1.3	0.9	1.0
Spot	42	115	2.0	1.3	2.0

[1]3.38 cal/mg O_2.
[2]Pinfish data from Hoss (1974), spot data from D. E. Hoss (pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.).
[3]Pinfish data from W. F. Hettler, Jr. (pers. commun., Atlantic Estuarine Fisheries Center, Beaufort, N.C.), spot data from Hoss et al. (1974).

values on a per unit weight basis are typical for larvae of different species. Such similarity, however, may not exist for all species and size classes.

Measurements of postlarval metabolic expenditures based on oxygen consumptions at 15°C using a Gilson respirometer (Hoss, pers. commun.) and a flowing water respirometer (W. F. Hetter, Jr., pers. commun., Atlantic Estuarine Fisheries Center) are shown in Table 5. In both cases, fish were deprived of food for 24 h prior to measurement of their oxygen consumption, and the oxygen content of the water was near air saturation. Both Hoss and Hettler consider their measurements to be routine oxygen consumption as defined by Fry (1971), i.e., the mean rate observed in fish whose metabolic rate is influenced by random activity under experimental conditions in which movements are presumably somewhat restricted and the fish are protected from outside stimuli. Postlarval pinfish and spot in the flowing water respirometer were confined in an 11-liter chamber identical to that used for our laboratory current-feeding experiments described earlier and therefore were able to move about considerably.

A major problem exists in most measurements of fish oxygen consumption due to the uncertainty as to the animals state of activity (Altman and Dittmer 1971). Furthermore, measurements of fish respiration under natural conditions, termed normal respiration, have been unattainable; and although many investigators have estimated normal respiration by doubling routine metabolism, such a process is felt to be too subjective by Hoss and Peters (in press).

Considering the requirement for information on fish metabolic needs under natural conditions, it appears that our method of estimating the daily rations of postlarval fishes has potential value. Our estimates of daily rations were higher or equal to those rations estimated from oxygen consumption measurements. The observed differences in rations (Table 5) are reasonable if we assume that oxygen consumption measurements, particularly those of Hoss, are closer to routine respiration than to normal. The Hoss data have the lowest values, followed by the Hettler data. These differences, although probably not significant, are reasonable because the less restrictive system provided in the flowing water respirometer allowed the fish to move about in a manner similar to that in natural water. The lack of feeding activity by fish during respiration measurements and the respective decrease in oxygen consumption (Warren and Davis 1967) also should account for a lesser daily ration.

Based on earlier metabolic measurements, Thayer et al. (1974) estimated a daily ration of 1.04 cal/fish per day for larval fishes in the Newport River estuary during January and February. They indicated that, with larval energy requirements of this magnitude and a 90% assimilation efficiency, the larvae would be required to graze on an average of 10% of the zooplankton population per day. Furthermore, they suggested that this need may indeed have accounted for decreases in zooplankton observed in the estuary during spring. Our daily rations, based on feeding periodicity and evacuation (Table 5), are somewhat larger and tend to support the conclusion, assuming larval densities similar to those presented by Thayer et al. that larval fishes may have a significant impact on copepod populations in this system.

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THERMAL TOLERANCE AND RESISTANCE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

GARY D. BREWER[1]

ABSTRACT

An experimental, flow-through seawater system, constructed to maintain juvenile and adult northern anchovy, *Engraulis mordax*, and rear embryos and larvae through yolk-sac absorption under controlled temperature and photoperiod regimes, was used to determine aspects of thermal tolerance, resistance, rates of acclimation, and some effects of temperature on the development and growth of the anchovy.

Thermal tolerance was determined for juvenile and adult fish, acclimated to six constant temperatures between 8° and 28°C. Thermal resistance (minutes until death for fish exposed to a lethal temperature) was independent of photoperiod and fish size; however, females proved more resistant than males, and resistance decreased at night. Acclimation (as measured by resistance) from 12° to 20°C was nearly complete after 2-day exposure to the higher temperature; acclimation from 20° to 12°C was nearly complete after 5-day exposure to the lower temperature. Fish subjected to fluctuating water temperatures between 12° and 20°C proved less resistant to cold than a 12°C (constant) acclimated group and less resistant to heat than a 20°C (constant) acclimated group.

Thermal tolerance was determined for larvae in the yolk-sac stage, acclimated to four constant temperatures between 12° and 24°C. Although hatching occurred at temperatures as high as 29.5°C and as low as 8.5°C, the percentage of normally developed larvae equaled that of controls (incubated at 16°C) only between temperatures of 27.0° and 11.5°C. Embryos in the blastodisc stage proved most sensitive to acute temperature increases when compared to embryos in the blastopore closure stage and larvae in the yolk-sac stage. These same three stages proved insensitive to acute temperature decreases to 0.5°C for 60-min exposure periods.

Temperature is discussed in relation to anchovy distribution and survival under natural and artificially created thermal conditions.

Research on the effects of temperature on aquatic organisms has been given impetus in recent years as numerous lakes and streams are considered potential heat reservoirs by electric power generating plants and other industrial concerns. As the demands for water as a heat transfer medium continue to increase dramatically, more attention will be turned to the marine environment for large volumes of water and surface areas necessary for the dissipation of excess heat (Naylor 1965; de Sylva 1969; Tarzwell 1972). Unchecked thermal loading of freshwater and nearshore marine ecosystems will inevitably pose a serious threat to the homeostasis and well-being of aquatic communities unless realistic guidelines are established and enforced. Such guidelines must be based on knowledge of how aquatic organisms respond to both acute and chronic temperature changes.

This study details aspects of thermal tolerance and resistance (as defined by Fry 1971) on the embryo, larval, juvenile, and adult stages of the northern anchovy, *Engraulis mordax* Girard. The study was prompted by the proposed discharge of thermal effluent into the Los Angeles-Long Beach Harbor. The biology and fishery of the northern anchovy in the Los Angeles-Long Beach Harbor were described by Brewer (1975a).

The general biology of the northern anchovy has been summarized by Baxter (1967), Messersmith et al. (1969), the California Department of Fish and Game (1971), and Brewer (1975a). A dramatic increase in abundance of *E. mordax* during the past 20 yr (Ahlstrom 1967; Smith 1972) has prompted an intense interest in the biology and fishery potential of this clupeoid. The California Department of Fish and Game (1971:48) considered the anchovy ". . . the most abundant species with immediate harvest potential in the California Current system."

MATERIALS AND METHODS

Experiments were conducted in a small, tem-

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perature and photoperiod controlled, flow-through seawater system. The system delivered filtered, ultraviolet-sterilized seawater from the Los Angeles-Long Beach Harbor to five round, 950-liter, fiber glass aquaria (1.5 m in diameter, 0.6 m high) and a single 400-liter rectangular water table, all housed in a light-tight aluminum cargo container (Figure 1). An exchange rate of 2-6 liters/min was maintained in each aquarium, with overflow drainage provided by standpipes. Wastewater was not recirculated. Temperatures were maintained within ±0.5°C.

Above each aquarium were two incandescent light bulbs controlled by separate dimmer controls and regulated by a 7-day timer to simulate photoperiods. The "day" bulb provided 700 lx and the "night" bulb provided 16 lx to the surface of each aquarium. Oxygen was maintained at or near saturation levels in all acclimation and test tanks by splashing incoming water at the surface and by bubbling air stones in the aquaria. Salinity varied between 31.4 and 33.8‰ (mean 33.1‰) during the study period.

Juveniles and Adults

Juvenile and adult *E. mordax* were obtained from a live-bait dealer. The initial transfer from the bait boat to the 950-liter acclimation tanks caused 20-30% mortality during the first 2-3 days of confinement. Within 2-4 days, healthy fish began to feed and were offered a daily ration, equivalent to approximately 4% of the fish's wet weight, of Trout Chow.[2] This ration was supplemented with chopped anchovy, chopped squid, brine shrimp, or wild plankton equal to approximately 1% of the fish's wet weight. Adjusted fish ate voraciously and mortality became insignificant in acclimation tanks within 1 wk. Acclimation tanks were stocked with between 3 and 7 kg of anchovy. The food ration was withheld for a period of 24 h prior to all thermal tests on juvenile and adult fish.

Ninety-six Hour Tolerance

Standardized techniques for the determination of lethal temperatures (Fry et al. 1942; Brett 1944; Fry 1947) call for a series of experiments in which the animals are acclimated to several different constant temperatures. Acclimated fish are then abruptly transferred to test aquaria previously equilibrated to various high and low temperature extremes. Mortality is monitored and recorded.

This procedure extends the concept of lethal temperatures from two extreme end points, to a family of upper and lower (incipient) lethal levels. The ultimate upper and lower lethal temperatures, which circumscribe the extreme tolerance limits, may be determined by graphic extrapolation—that is, by drawing a line through those high and low test temperatures that proved lethal to 50% of the test animals for each acclimation temperature. The extrapolated line will then

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

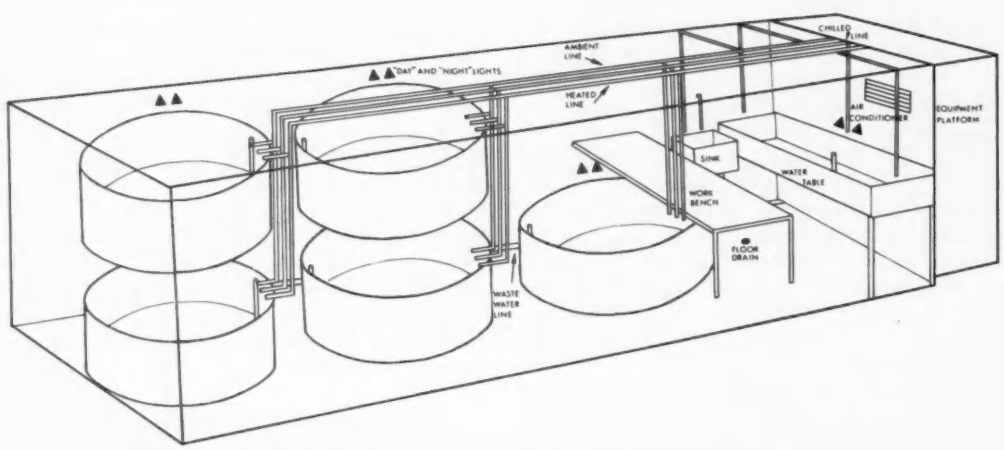

FIGURE 1.—Diagram of the flow-through seawater system used for experiments on *Engraulis mordax*.

intersect a diagonal at the upper and lower extremes, which represents those points where the lethal temperatures equal the acclimation temperatures. Fish cannot be acclimated to temperatures above or below these experimentally determined ultimate upper and lower lethal temperatures, respectively.

Juvenile and adult *E. mordax* between 45 and 139 mm SL (standard length) were held for a minimum of 3 wk at constant temperatures of 8°, 12°, 16°, 20°, 24°, and 28°C and under a light cycle of 12 h light and 12 h dark. Unless otherwise noted, the term "acclimated fish" designates *E. mordax* held under such conditions. "Juvenile" refers to metamorphosed fish less than 100 mm SL, while "adult" refers to fish over 100 mm.

The fish's susceptability to mechanical damage increased at high and low acclimation temperatures. Therefore, each acclimation temperature-test series was accompanied by a series of strict control transfers, and the observed mortalities for each series were adjusted separately, based on the respective control mortalities. Fish were considered dead and were removed when all swimming movements ceased. Ninety-six hour LD_{50} (mean lethal dose) temperatures (i.e., incipient lethal levels) were estimated from regression lines plotted on probit paper (Sokal and Rohlf 1969). Experiments were conducted between February 1973 and November 1974 and included all seasons. About 20 fish were used for each test.

Resistance as a Function of Size, Sex, Time, and Photoperiod

To test the potential influence of photoperiod, sex, size, and diel effects, anchovies were acclimated to 20°C, tested by direct transfer to 30°C, and the time to death (resistance time) determined. As the fish died, they were removed from the test aquaria, measured, and adult fish were sexed. Identical tests were conducted in the morning (0900 h) and in the evening (2100 h). Tests were also conducted after fish had been held under a short-day photoperiod (8 h light) and a long-day photoperiod (16 h light) for periods of 3 wk each. All thermal resistance tests were run during the summer and fall.

Rates of Thermal Acclimation

Juvenile and adult anchovy acclimated to 12°C were subjected to an 8°C temperature change over a 24-h period to 20°C, and then tested for resistance to 30°C on the same day and after 1-, 2-, and 4-day exposure to the 20°C temperature. Moreover, fish acclimated to 20°C were subjected to a temperature decrease to 12°C over a 24-h period, and then tested for resistance to 6°C on the same day and after 2-, 5-, and 9-day exposure to the 12°C temperature. As the fish become acclimated to the new higher or lower temperature, one would expect the mean resistance times for these fish to approach and eventually equal the mean resistance times (e.g., reach a steady-state) of fish acclimated to 20° and 12°C and tested at 30° and 6°C, respectively (controls).

Effects of Cycled Temperatures on Resistance

In view of the observations by Mais (1974) that *E. mordax* may undergo diel vertical migrations and consequently experience fluctuating temperatures, I examined the relative thermal resistance of anchovies subjected to regular changes in temperature from 12° to 20°C over 48-h intervals. Fish acclimated to 20°C were gradually subjected to decreasing temperatures to 12°C over 24 h and then back to 20°C over the next 24 h. The cycle was repeated for 25 days, at which time a sample of fish which had just reached 20°C was tested for resistance to 30°C. The following morning, as the remaining fish reached 12°C, a sample was tested for resistance to 6°C.

Embryos and Larvae

Engraulis mordax eggs, caught in plankton tows in or near the Los Angeles-Long Beach Harbor throughout the year, were utilized for experiments on embryos and larvae. Water temperatures, at time of capture, varied between 13° and 18°C. In the laboratory, eggs in the blastodisc stage were placed into 2-liter glass jars and maintained at 12°, 16°, 20°, or 24°C until transferred to incubation or test vessels which consisted of 250-ml jars containing 60 ml of seawater. Not more than five eggs or larvae were tested per jar.

Twenty-four Hour Tolerance

Larvae in the yolk-sac stage were tested within 1 day after hatching at each acclimation temperature. Larvae were pipetted from each acclimation temperature directly into test vessels ranging

from 6° to 32°C. Mortality was recorded after 24 h. Incipient lethal levels for each acclimation level were estimated as described for the juveniles and adults.

Hatching and Developmental Temperature Limits

Eggs in the blastodisc stage were transferred to a series of incubation vessels, after which the temperatures were gradually raised or lowered from the ambient level of 16°C over a period of 60 min in order to avoid possible shock effects to the developing embryos. Incubation temperatures were then held constant (±0.5°C) between 6° and 12°C, and 26° and 31°C at 0.5°C intervals. A 16°C temperature was used as a control. Development was considered normal only if the larvae were free of obvious deformities (e.g., spinal curvatures) until pigmented eyes and functional jaws were evident, and death had occurred only after yolk reserves were exhausted.

Resistance to Acute Temperature Changes

Embryos in the blastodisc stage (ca. 12-14 h after fertilization at 16°C) and in the blastopore closure stage (ca. 36-38 h after fertilization), and larvae in the yolk-sac stage (within 24 h after hatching) were subjected to temperature shocks for periods of 1, 3, 5, and 60 min. Embryos and larvae were pipetted from incubation vessels maintained at 16°C directly into water at high and low temperature extremes. After the exposure period, the embryos and larvae were returned directly to the incubation vessels at 16°C where they remained for 48 h after hatching. Mortality and developmental abnormalities were recorded.

This procedure was an attempt to simulate what the embryos and larvae might actually experience if entrained by intake pipes of electrical generating plants or LNG (Liquified Natural Gas) vaporization plants (or either thermal plums), subjected to rapid temperature increases and decreases in the heat exchange systems, and subsequently flushed back into the natural environmental temperatures at the outfall.

Development and Growth

Experiments were designed to determine the temperatures required for optimal growth of anchovy larvae. The tests were confined to that period of larval life between hatching and starvation following exhaustion of all stored yolk reserves. No food was offered.

Eggs in the blastodisc stage were reared through hatching in a series of constant temperature baths between 10° and 26°C. On the day of hatching and each subsequent day, approximately 10 larvae were sacrificed from each rearing temperature and measured from the tip of the snout to the end of the notochord with an ocular micrometer to the nearest 0.05 mm. This procedure was continued until all larvae at each rearing temperature died of starvation.

RESULTS

Juveniles and Adults

Ninety-six Hour Tolerance

Experiments on juvenile and adult tolerance encompassed 117 separate 96-h tests and 2,400 fish. Control survival ranged from lows of 81.3 and 87.9% at 8° and 28°C acclimation temperatures, respectively, to 98.3% at the 16°C acclimation temperature.

Figure 2 graphically depicts the lethal temperature relations, with adjusted percent mortality plotted against test temperatures for acclimation levels of 8° and 28°C. Adjusted upper and lower LD_{50} temperatures were plotted against acclimation temperatures in Figure 3 and a thermal tolerance polygon constructed (Fry 1947). Ultimate upper and lower lethal temperatures are estimated by extrapolation (line fitted by eye) to be

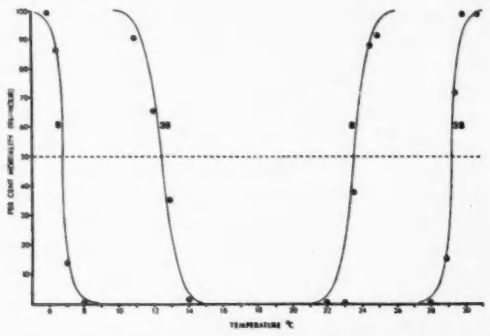

FIGURE 2.—Effects of acclimation temperatures of 8° and 28°C on the upper and lower lethal temperatures of *Engraulis mordax* juveniles and adults (original date in Brewer 1975b).

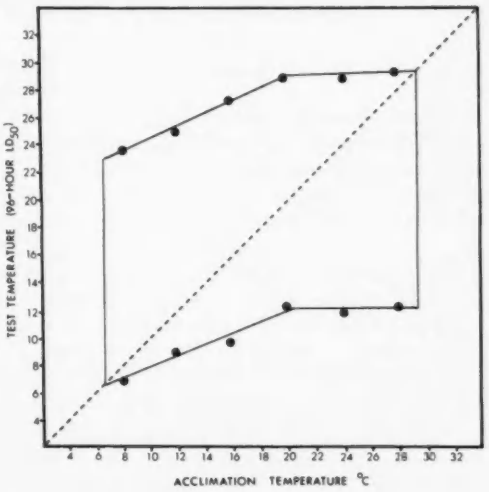

FIGURE 3.—Thermal tolerance polygon for *Engraulis mordax* juveniles and adults. Those points where the extrapolated LD_{50} levels intersect the diagonal represent the extreme (ultimate) tolerance limits and correspond to 6.5° and 29.5°C.

29.5° and 6.5°C, respectively. These temperatures represent the maximum tolerance range of *E. mordax* juveniles and adults sampled from southern California and maintained under laboratory conditions as described. Anchovy cannot be acclimated to temperatures beyond these extremes. Attempts were made to slowly acclimate fish to 29.5° and 6.5°C, but they proved futile.

Figure 4 shows the resistance times to median mortality of juvenile and adult *E. mordax*, acclimated to 8°, 16°, and 28°C, upon exposure to temperatures beyond incipient lethal levels. These curves were derived by plotting cumulative mortality as percentages against exposure time to estimate the time to LD_{50} for each test temperature.

Resistance as a Function of Size, Sex, Time, and Photoperiod

Results of experiments on thermal resistance to 30°C in relation to size, sex, and potential diel and photoperiod effects are summarized in Table 1. Analysis of variance (one-way classification) showed that resistance times to lethal temperatures of 30°C were not significantly different ($P>0.05$) for fishes of different sizes (<79 mm; 80-99 mm; >100 mm) or for fishes maintained under different photoperiods (8, 12, and 16 h

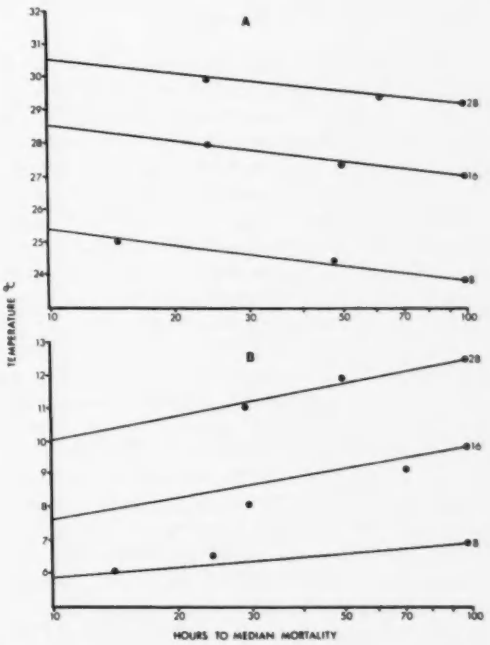

FIGURE 4.—Resistance times to median mortality of juvenile and adult *Engraulis mordax* exposed to high (A) and low (B) lethal temperatures when acclimated to 8°, 16°, and 28°C.

TABLE 1.—Comparison of resistance times (minutes until death) for juvenile and adult *Engraulis mordax* acclimated to 20°C and immediately transferred to aquaria at 30°C.

Item	N	Range (min)	Mean (min)	SD	SE
Length (mm):					
<79	11	49-285	133.9	74.9	22.6
80-99	22	41-302	149.4	62.3	13.3
>100	12	37-343	141.3	102.9	29.7
Sex:					
Male	20	6-118	40.9	33.1	7.4
Female	36	4-401	116.8	113.6	18.9
Time of test:					
Morning	45	31-343	143.5	76.3	11.4
Evening	38	8-244	72.6	66.7	10.8
Photoperiod (hours of light):					
8	14	6-401	154.5	127.0	34.0
12	34	37-302	141.1	67.6	11.6
16	11	31-343	150.8	102.3	30.9

light). These results should be verified with larger sample sizes. Resistance times showed highly significant differences ($P<0.01$) for males compared with females, and for tests conducted in the morning as compared with those conducted at night. Females proved more resistant than males, and animals tested in the morning showed greater resistance than those tested in the evening.

Rates of Thermal Acclimation

Results suggest that acclimation from 12° to 20°C nears completion within 2 days of exposure to the higher temperature. Mean resistance times for day 2 and day 5 samples exceeded the mean resistance time for the control sample. However, analysis of variance shows that the variation between day 2, day 5, and control samples is not significant ($P>0.05$). The relatively high resistance of some fish in the day 2 and day 5 samples, which exceeded the resistance of control fish, may be due to slight temperature variations (±0.2°C) in the test aquaria, or possibly to "physiological overshoots" to the acclimation process (Prosser 1973). Figure 5 shows the progress toward acclimation with contined exposure to the higher temperature. Most noticeable is the change in shape of the resistance curves with acclimation. Nonacclimated fish succumb to the lethal 30°C temperature quickly, probably as a result of "shock effects" (Scott 1964; Tyler 1966; Allen and Strawn 1971). Acclimation to the higher temperature diminishes the shock effects. Apparently, acclimated fish die from secondary causes termed "direct effects" by Fry (1971). The physiological basis of the shock and direct effects is not clear. Acclimation from warm to cool water (20° to 12°C) appears to be nearly complete by day 5 (Figure 6). As acclimation progresses and resistance to low temperatures is increased, death rate becomes increasingly regular; the graphs approach a straight line and the effects of the initial cold shock are largely eliminated. Because these tests used small sample sizes, statistical differences cannot be demonstrated.

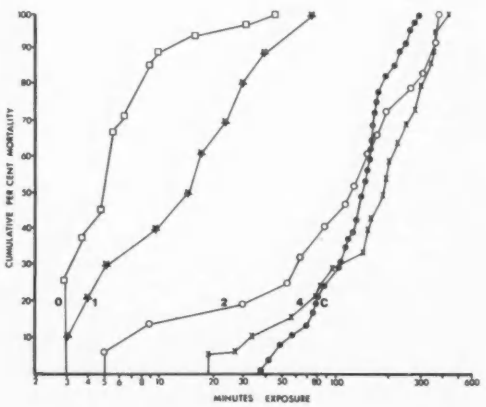

FIGURE 5.—Cumulative percent mortality of *Engraulis mordax* juveniles and adults as a function of exposure to 30°C. The response of a 20°C acclimated control group (C) is compared with that of a 12°C acclimated group after 0-, 1-, 2-, and 4-day exposures to 20°C (original data in Brewer 1975b).

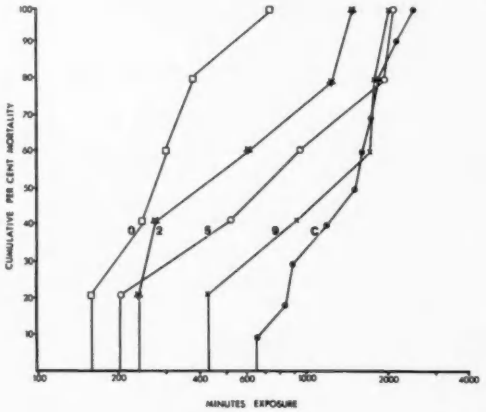

FIGURE 6.—Cumulative percent mortality of *Engraulis mordax* juveniles and adults as a function of exposure to 6°C. The response of a 12°C acclimated control group (C) is compared with that of a 20°C acclimated group after 0-, 2-, 5-, and 9-day exposures to 12°C (original date in Brewer 1975b).

Effects of Cycled Temperatures on Resistance

Results are summarized in Table 2. Mean resistance times to 6° and 30°C for fish subjected to periodic changes in temperature between 12° and 20°C were well below the mean resistance times of fish acclimated to a constant 12°C and constant 20°C, respectively. However, the fish have greater high temperature resistance than those acclimated to 12° and greater low temperature resistance than those acclimated to 20°C.

TABLE 2.—Resistance times (minutes until death) of juvenile and adult *Engraulis mordax* to 6° and 30°C after being subjected to temperature fluctuations between 12° and 20°C on a 48-h cycle for a period of 25 days.

Test temp	Group	*N*	Range (min)	Mean (min)	SD	SE
6°C	12°C acclimated	10	643-2,490	1,419.0	589.0	186.3
	20° to 12°C	10	117-1,111	410.6	374.5	118.4
30°C	20°C acclimated	34	37-302	141.1	67.6	11.6
	12° to 20°C	10	6-68	28.0	22.1	7.0

Embryos and Larvae

Twenty-four Hour Tolerance

Over 600 larvae were tested in the 24-h tolerance experiments. Generally, 10 or more larvae were tested at each temperature. The percentage (normal) survival for controls ranged from 72.7 at the 12°C acclimation level to 86.7 at 16° and 20°C acclimation temperatures.

Apparently the physiological mechanisms for thermal acclimation are little developed in *E. mordax* larvae in the yolk-sac stage. Figure 7 shows the 24-h lethal temperature relations with percent adjusted mortality plotted against test temperatures for acclimation temperatures of 12° and 24°C. Rearing the yolk-sac larvae in warm and cold water does little to increase or decrease their upper or lower lethal temperatures, respectively. Potential effects of parental acclimation temperatures (Hubbs and Bryan 1974) or the exposure of eggs to acclimation temperatures at the time of fertilization require investigation.

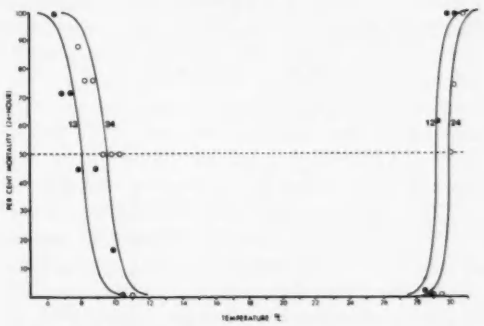

FIGURE 7.—Effects of acclimation temperatures of 12° and 24°C on the upper and lower lethal temperatures of *Engraulis mordax* larvae in the yolk-sac stage (original data in Brewer 1975b).

In Figure 8, adjusted upper and lower LD_{50} temperatures are plotted against respective acclimation temperatures in the construction of a thermal tolerance polygon. Ultimate upper and lower lethal temperatures are estimated to be 30.2° and 7.0°C, respectively.

Hatching and Developmental Temperature Limits

Results of this experiment are given in Table 3. Although hatching was observed at temperatures as high as 29.5°C and as low as 8.5°C, 50% (adjusted) normal development occurred between 11.0° and 28.5°C. Only below 27.0°C and above 11.5°C did the percentages of hatching and normal development approach those for the controls.

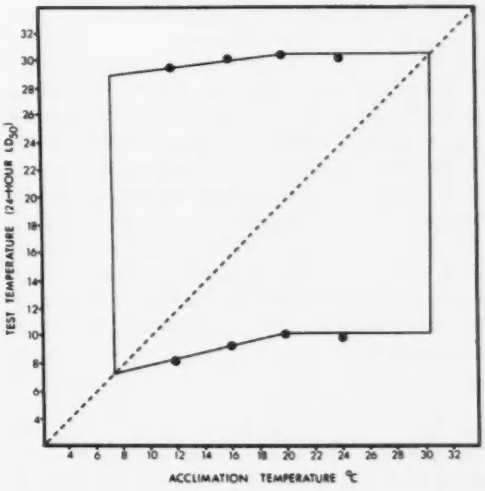

FIGURE 8.—Thermal tolerance polygon for *Engraulis mordax* larvae in the yolk-sac stage. Those points where the extrapolated LD_{50} levels intersect the diagonal represent the extreme tolerance limits and correspond to 7.0° and 30.2°C.

TABLE 3.—Effects of temperature on hatching and development of *Engraulis mordax* through yolk-sac absorption and eye pigmentation of larvae. Temperatures were maintained within ±0.5°C of those shown below.

Rearing temp (°C)	N	No. hatching	With normal development		Adjusted survival (%)
			No.	%	
31.0	10	0	0	0	0.0
30.0	10	0	0	0	0.0
29.5	10	3	3	30.0	33.3
29.0	10	3	3	30.0	33.3
28.5	10	8	5	50.0	55.6
28.0	30	27	23	76.7	84.9
27.5	10	9	7	70.0	77.8
27.0	30	28	27	90.0	100.0
26.5	10	8	8	80.0	88.9
26.0	10	9	9	90.0	100.0
[1]16.0	30	29	27	90.0	100.0
7.5	10	0	0	0.0	0.0
8.0	10	0	0	0.0	0.0
8.5	10	2	0	0.0	0.0
9.0	10	3	0	0.0	0.0
9.5	15	3	0	0.0	0.0
10.0	10	6	1	10.0	11.1
10.5	10	5	3	30.0	33.3
11.0	10	8	6	60.0	66.7
11.5	10	9	9	90.0	100.0
12.0	10	10	9	90.0	100.0

[1]Control.

Resistance to Acute Temperature Changes

Resistance to high temperatures is surprisingly great for embryos and larvae when exposure is of short duration (Figure 9). Blastodisc stage embryos are least resistant while yolk-sac larvae are most resistant; LD_{50} values for the 60-min exposure period for the larvae are within 1.3°C of the extrapolated 24-h tolerance limits determined from Figure 8. *Engraulis mordax* embryos and larvae appear to be insensitive to abrupt temperature decreases down to 0.5°C for short periods (Brewer 1975b).

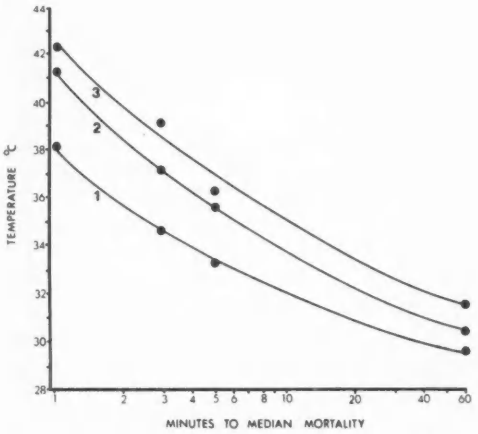

FIGURE 9.—Minutes to median mortality for the blastodisc stage (1), blastopore closure stage (2), and yolk-sac stage (3) subjected to abrupt temperature increases from 16°C (original data in Brewer 1975b).

Development and Growth

Table 4 summarizes data on the growth of larvae at constant temperatures between 10° and 26°C. The maximum size of larvae attained at any temperature before shrinkage due to starvation was 4.16 mm. This is considerably smaller than the value of 4.8 mm given by Lasker (1964) for *E. mordax* larvae reared under similar conditions. Variability in egg size may be responsible for this discrepancy; egg size of the Argentine anchovy, *E. anchoita*, is known to vary by season and location (de Ciechomski 1973).

The highest mean growth response was obtained for larvae reared at 18°C (3.94 mm). Mean larval lengths less than 3.78 mm were considered significantly smaller than the maximum response at 18°C (Least Significant Difference, Sokal and Rohlf 1969). It seems reasonable to assume that larvae reared at temperatures of 12°C or lower and 24°C or higher converted yolk into body tissue at suboptimal levels. Analysis of variance showed that maximum mean lengths attained by larvae reared at 14°, 17°, 18°, and 20°C were not significantly different ($P>0.05$).

TABLE 4.—Comparison of the maximum size attained by *Engraulis mordax* larvae in the yolk-sac stage before shrinkage due to starvation.

Incubation temp (°C)	N	Range (mm)	Mean (mm)	SD	SE
10	10	3.37-3.79	3.63	0.13	0.04
12	10	3.31-4.00	3.62	0.21	0.07
14	10	3.63-4.10	3.93	0.18	0.06
17	10	3.63-4.00	3.81	0.15	0.05
18	10	3.63-4.10	3.94	0.16	0.05
20	10	3.52-4.16	3.82	0.18	0.06
24	10	3.52-4.00	3.71	0.14	0.04
26	10	3.42-3.84	3.56	0.13	0.04

DISCUSSION

Figure 10 shows a graphic summary of various field and laboratory-deduced temperature ranges and limits for the distribution and survival of *E. mordax*. A temperature range of about 4.5°C lies between the highest temperatures that anchovy adults have been found in nature (25°C, Baxter 1967) and the experimentally determined upper lethal temperature for juveniles and adults (29.5°C). Anchovy had been maintained in the laboratory at 28°C for weeks with no apparent ill effects. The fish are extremely active at this temperature and their metabolic requirements are undoubtedly considerable. Anchovy maintained at 28°C and fed the standard ration lost weight. The upper environmental temperature limit and southern distributional limit of *E. mordax* may be dictated by metabolic demands which outweigh the ration supplied by the environment. Maximum temperatures off Cabo San Lucas, which is the southern range limit for *E. mordax*, exceeds 25°C (Lynn 1967). Interestingly, 25°C corresponds to the highest temperature that juvenile *E. mordax* would venture into when tested in laboratory thermal gradients (Brewer 1974). Moreover, the plateau in the thermal tolerance polygon (Figure 3) shows that acclimation temperatures of 24°C and above have little effect on increasing the incipient upper lethal temperature. Apparently the anchovy's overall mechanisms for

physiological compensation begin to break down at temperatures above 25°C.

Reid's (1967) observation that *E. mordax* may overwinter at temperatures of 7° or 8°C off British Columbia is of special interest. These fish may be within less than 1°C of their lower lethal temperature. Juvenile and adult anchovy acclimated to 8°C in the laboratory and transferred to 7°C made no effort to consume food offered to them after 5 days at the lower temperature. I have not confirmed this by stomach examination, but feeding, if it takes place at all, is minimal at this low temperature.

It is important to consider the possibility that the thermal tolerance and resistance of *E. mordax* may be different for northern, central, and southern populations. Apparently genetically distinct, these populations were first identified on the basis of meristic characters by McHugh (1951) and later on by serum transferrin analysis conducted by Vrooman and Smith (1971). If the thermal requirements of these populations were distinct, I would anticipate their reproductive temperature ranges to vary accordingly. Richardson's (1973) data on anchovy spawning off Oregon discount this. In any case, thermal resistance experiments on samples from each population would be of interest.

Experiments on the resistance of juvenile and adult anchovy to a high lethal temperature showed no significant difference in the mean resistance times for fish of different sizes or for fish maintained under different photoperiods. However, females were more resistant than males, and animals tested in the morning showed greater resistance than those tested in the evening. Investigators have variously shown significant differences in one or more of the factors tested here, depending on the species. Thermal resistance has been found to vary according to size, with large *Oncorhynchus* (Salmonidae) and *Carassius* (Cyprinidae) more resistant to cold (Brett 1952; Hoar 1955, respectively) and large *Clupea* (Clupeidae) less resistant to heat (Brawn 1960). *Carassius* maintained under long photoperiods were more resistant to high temperatures than fish maintained under short photoperiods, while resistance to cold temperatures was greater for the short photoperiod fish (Hoar 1956). Hoar discovered that male *Carassius* were more resistant to low temperature extremes than females. Heath (1963) observed slight differences in critical thermal

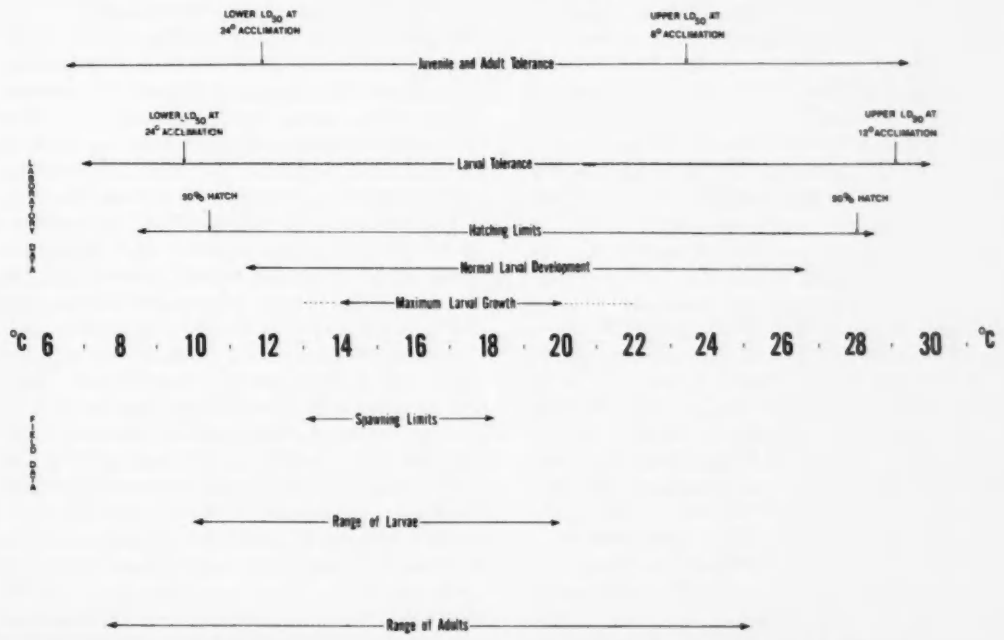

FIGURE 10.—Field and laboratory deduced thermal limits for the distribution and survival of *Engraulis mordax*.

maximum temperatures for *Salvelinus* (Salmonidae), depending on the time the test was conducted. He also noticed that maximum tolerance followed a 24-h cycle and suggested that this was a physiological adaptation to natural habitats with 24-h variations in temperature.

The present experiments on *E. mordax* were conducted in the fall when anchovy presumably ascend from deep water to warm surface waters in the evening (California Department of Fish and Game 1971). If a circadian cycle of thermal resistance existed in anchovy, one might anticipate maximum resistance to high temperatures to occur in the evening. The data in Table 1 suggest that, under laboratory conditions, resistance to high temperature is reduced in the evening.

The embryonic and larval stages of pelagic fishes are potentially the most vulnerable ones to thermal stresses. While juvenile and adult fishes may detect and avoid unfavorable environmental conditions (Bull 1928; Doudoroff 1938; Alabaster and Robertson 1961; Coutant 1969), the eggs and planktonic larvae of fishes such as *E. mordax* are at the mercy of currents which might carry them into environments unfavorable for growth or survival. Reviews by de Sylva (1969) and Brett (1970) have shown that on the average, marine fish larvae are one-third to one-half as tolerant to thermal stresses as their conspecific adults. Normal development of *E. mordax* is inhibited below 11.5°C and above 27.0°C. Larvae held at temperatures below 11.0°C for short periods become inactive, making little effort to avoid capture by pipette.

The survival of pelagic larvae is dependent on the early consumption of prey species and the ability to avoid predators (Lasker et al. 1970). The degree to which these two processes can be accomplished is largely dependent on the optimal development of swimming ability, precise biting reflexes, and visual acuity (Hunter 1972). Since swimming ability is proportional to larval size, the development of maximum growth potential should be of distinct survival value. Maximum growth of larvae in the yolk-sac stage, in turn, is dependent on the efficient utilization of the limited yolk reserve, i.e., its conversion into body tissues.

Growth of anchovy larvae in the yolk-sac stage is maximal in experimental temperatures between 14° and 20°C. Variation within this range may be highly significant but is difficult to test. Although growth rates of anchovy larvae in the yolk-sac stage increase with increasing temperatures, the maximum size attained by the larvae decreased at high temperatures.

Thermal tolerance limits have been determined for anchovy larvae and juveniles and adults by tests that considered the LD_{50} as a lethal end point. LD_{50} temperatures do not represent "safe" levels and have been used merely because of convention. Any temperature level that produces a lethal response significantly greater than the maximum response at control temperatures should be considered excessive. This would represent the most realistic end point to insure environmental quality. The thermal death of even a few individuals at any particular temperature level suggests that the survivors are under severe stress, leaving them unable to compete successfully for limited resources or avoid predation. For acclimation temperatures of 8°, 12°, 16°, 20°, and 24°C, a range of temperatures encountered by juveniles and adults in nature, immediate exposure to high temperatures less than 23.0°, 24.0°, 25.5°, 26.5°, and 27.5°C, respectively, would be tolerated by fish from southern California without significant mortality from the direct effects of temperature alone. Likewise, for the same acclimation temperatures, juvenile and adult anchovy could tolerate lows of 7.5°, 10.0°, 12.5°, 13.5°, and 14.5°C, respectively. Larvae in the yolk-sac stage can tolerate limited exposure (24 h) to any temperature <28.0°C and >12.0°C. Regardless of acclimation temperature, larvae in the yolk-sac stage, juveniles, and adults can endure sudden temperature increases and decreases between the limits of 14.5° and 23.0°C without significant lethality from direct temperature effects alone.

Although the gross effects of high and low temperature extremes have been quantified, the physiological and biochemical factors that are responsible for thermal death and temperature acclimation are poorly understood. Various mechanisms to account for these phenomena have been discussed by Hochachka and Somero (1971) and Hazel and Prosser (1974). Evidence suggests that qualitatively different enzymes (isoenzymes) may be synthesized during thermal acclimation, and "warm" and "cold" enzyme variants have been described (Hochachka 1967; Hochachka and Somero 1968; Hebb et al. 1969). Enzyme inactivation has been suggested as a cause of thermal death, but it is ". . . undoubtedly more subtle than gross protein denaturation" (Hochachka and Somero 1971:139). The reaction velocities (K_m) of enzymes may drop below certain critical levels at

high and low temperatures, resulting in the disruption of basic physiological functions such as osmoregulation, respiration, and overall nervous system integration (Prosser 1973).

It is unlikely that the offshore realm of any ocean could ever be significantly affected by artificial thermal input. Projected energy needs for the decades ahead and their associated requirements for immense volumes of water for cooling (electric power generating) and heating (LNG) may pose a serious environmental threat in nearshore areas, especially bays, harbors, and estuaries. As a case-in-point, juvenile northern anchovy find the confined waters of the Los Angeles-Long Beach Harbor a suitable habitat. Brewer (1975a) found anchovy egg densities as high as 35/m^3 of surface water within 0.5 mile of the harbor breakwater. These areas will be affected by seawater intake pipes, and thermal effluent plumes and *E. mordax* embryos would be highly susceptible to entrainment. Eggs in the blastodisc stage are most sensitive to abrupt changes in temperature. If one considers the high temperature extremes where mortality begins to exceed the control mortality as unsafe, anchovy embryos should not be allowed to remain in temperatures of 35.5°, 30.5°, 30.0°, and 27.5°C for periods longer than 1, 3, 5, and 60 min, respectively. While embryos proved insensitive to the effects of temperatures as low as 0.5°C for 60-min exposures, it is questionable whether these sensitive developmental stages could withstand the turbulence and mechanical shock associated with heat exchange systems or thermal effluent outfalls. In this respect, larvae are most vulnerable, and Lasker (1964) found this vulnerability increased with decreasing temperatures below 14°C for Pacific sardine, *Sardinops*, larvae which are morphologically similar to anchovy larvae. Their thin integument and fragile bodies are easily damaged. Extreme care was taken in the present study when the larvae were transferred from incubation to test jars, but control survival was only 77.5%. Survival of larvae in experiments that did not involve transfer to rearing vessels was over 90%. Serious consideration must therefore be given to the location of intake pipes and effluent discharge to avoid trapping eggs and larvae. These stages are probably too small to be excluded by screening.

Many more experiments are required to understand the dynamics of the thermal requirements of *E. mordax*. It may be unreasonable to assume that there is one optimal temperature for anchovy well-being. Activity cycles or rhythms (e.g., the evening spawning cycle) may be present in natural populations which require diel temperature changes (e.g., achieved through vertical migration). Temperature optima for reproduction or the growth of larvae in the yolk-sac stage may differ from optima for growth of juveniles and adults which must respond to fluctuating food levels. Brett et al. (1969), experimenting with *Onchorhynchus nerka*, found that as food rations were decreased, temperatures required for maximum growth rates also decreased. When food rations were not limiting, growth rates increased as the temperature increased to a certain optimal level, after which growth rates decreased rapidly.

In conclusion, the potential responses of the northern anchovy to temperature are many and varied. They depend upon the degree and rate of temperature change, length of exposure to a particular temperature, the previous thermal experience of the fish, and the effects of interactions among other environmental variables, both biotic and abiotic. Furthermore, these responses vary with ontogeny.

Although expatriated individuals may temporarily tolerate environmental extremes, the distribution and survival of *E. mordax* are ultimately dependent upon those physicochemical characteristics of the environment conducive to spawning. For the present, such an environment is best described as that part of the California Current where surface water temperatures reach 13°-18°C during at least part of the year (Ahlstrom 1956, 1959, 1966, 1967; Richardson 1973).

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NOTES

ISOLATION AND DESCRIPTION OF TWO VIBRIOS PATHOGENIC TO PACIFIC SALMON IN PUGET SOUND, WASHINGTON

Vibrio anguillarum (Bergman 1909) is recognized worldwide as a saltwater pathogen in fish (Anderson and Conroy 1970). Most epizootics caused by marine bacteria have been attributed to this organism (Rucker 1959; Sindermann 1966). This note describes recent mortalities resulting from vibriosis of Pacific salmon in the marine waters of Puget Sound, Wash., and heterogeneity observed in vibrios isolated from diseased fish.

The National Marine Fisheries Service (NMFS) is engaged in the experimental culture of Pacific salmon in salt water at the NMFS Aquaculture Experiment Station near Manchester, Wash. Epizootics caused by marine vibrios have occurred regularly in cultured salmon during the spring and summer months; the organisms were also isolated from diseased fish on a minor scale in every month during fall and winter (Novotny 1975). Vibrios originally isolated from diseased fish at Manchester were typical of *Vibrio anguillarum* (Evelyn 1971); strain 775 was representative.

In November 1973, a commercial salmon farm in the Manchester area suffered a high mortality of pen-reared, 0-age, 250-g coho salmon, *Oncorhynchus kisutch*. Past experience with vibriosis in the area indicated that the first serious outbreaks usually began in April when water temperatures exceeded 9°C and continued until water temperatures dropped below 12°C in early October (Novotny 1975). Water temperatures in November 1973 were 10° to 11°C; therefore, problems from vibriosis were not anticipated.

Mortalities also began to occur at about the same time, although not on an epizootic scale, in coho salmon held at the NMFS facility at Manchester. These fish had been vaccinated in late spring by injecting a heat-killed bacterin prepared from *V. anguillarum* 775. Oral antibiotics were administered, but the period required to bring the disease under control appeared to be almost twice that usually required for *V. anguillarum*.

Diseased fish sampled from the NMFS pens and the commercial farm exhibited the common signs of vibriosis, most notably a hemorrhagic septicemia. Bacteria characterized as vibrios were consistently isolated from dead or dying fish, but the growth rate of the isolated bacteria was markedly different from that of the typical *V. anguillarum*. Also, this bacterium was not agglutinated by rabbit anti-*V. anguillarum* 775 serum in rapid slide agglutination tests.

The new isolates were confirmed as pathogens by injecting pure cultures of them into salmon. All the injected fish died and the organism was routinely re-isolated from kidneys. We designated this bacterium as *Vibrio* sp. 1669.

In June 1974, NMFS conducted cooperative vaccination tests with a second commercial salmon farm in the Manchester area. Approximately 280,000 coho salmon smolts were injected with a heat-killed bacterin of *V. anguillarum* 775 at least 2 wk prior to their transfer to saltwater pens. Mortalities were exceptionally low until late August (less than 6% from all causes and less than 2% from vibriosis). At that time the rate of mortality began to increase and *Vibrio* sp. 1669 was isolated.

Further tests were made in early August 1974, when 450 0-age sockeye salmon, *O. nerka*, smolts were transferred to NMFS saltwater pens. One pen contained 150 unvaccinated control fish, and two pens contained 150 fish each that had been vaccinated in fresh water with a heat-killed *V. anguillarum* 775 bacterin. After 50 days in the saltwater pens, 95% of the unvaccinated fish had died. During the same period the mortalities in the vaccinated lots were 9% and 27% (Figure 1). Vibrios isolated from the vaccinated fish were only of the 1669 type, based on results of slide agglutination tests.

Materials and Methods

Samples of kidney, eye, or spleen from freshly dead or moribund fish were streaked on trypticase soy agar (TSA) (Difco)[1] with 1% salt added, or on 50% seawater cytophaga agar (Pacha and

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

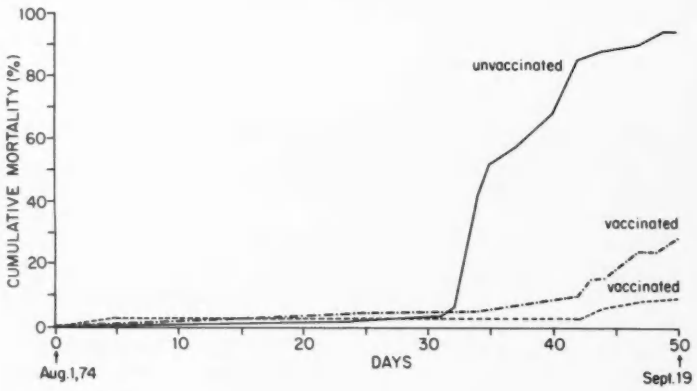

FIGURE 1.—Comparative rate of mortality of three lots of 0-age sockeye salmon raised in net pens at Manchester, Wash. Two of the lots were vaccinated with an intraperitoneal injection of a heat-killed bacterin prepared from *Vibrio anguillarum* 775.

Ordal 1967). Plates were incubated aerobically at 23°C. Presumptive identifications of the bacteria were based on the following tests: gram stain, motility and morphology characteristics under phase contrast microscopy, oxidase test (Kovacs), fermentation or oxidation of glucose, and sensitivity to the vibriostatic compound 0/129 (2,4-diamino-6,7-diisopropyl pteridine phosphate).

Further biochemical characterization included tests in Moeller's media for an alkaline reaction with arginine and for lysine decarboxylase, the production of indole, the production of acetylmethylcarbinol (Voges-Proskauer test), and the ability to ferment arabinose, glycerol, mannitol, sucrose, and galactose. These tests were selected because they were found to be variable among marine vibrio groups established by deoxyribonucleic acid homology characteristics (E. J. Ordal, University of Washington School of Medicine, Seattle, pers. commun.). In all of these tests additional NaCl (1%) was added.

TABLE 1.—Selected properties of *Vibrio anguillarum* 775 and *Vibrio* sp. 1669.

Property	*V. anguillarum* 775	*Vibrio* sp. 1669
Gram reaction	–	–
Motility	+	+
Oxidase (Kovacs) test	+	+
Fermentative (glucose)	+	+
Gas from glucose	–	–
Moeller's media:		
Arginine-alkaline reaction	+	–
Lysine decarboxylase test	–	–
Indole production	–	–
Voges-Proskauer reaction	+	–
Acid from:		
Arabinose	+	–
Glycerol	+	–
Mannitol	+	+
Sucrose	+	+
Galactose	+	–

Antisera for serological comparisons were prepared in both rabbits and coho salmon with heat-killed bacterins of *V. anguillarum* 775 and *Vibrio* sp. 1669 in Freund's complete adjuvant. Rapid slide agglutination tests with the specific antisera were used for initial differentiation. The microtiter system (Cooke Engineering Co.) was used later to determine agglutinin titers, and immunodiffusion techniques were used to further compare antigenic structure and relatedness. Tests were run with unabsorbed antisera and with anti-*Vibrio* sp. 1669 sera absorbed with *V. anguillarum* 775.

Results and Discussion

Vibrio sp. 1669 was typical of the marine vibrio group: it was characterized as a gram negative, motile, curved, asporogenous rod that was oxidase positive, an anaerogenic fermenter, and sensitive to the vibriostatic compound 0/129. A slower rate of growth of *Vibrio* sp. 1669, in comparison to *V. anguillarum* 775, was observed on TSA, as well as variations in certain culture reactions (Table 1).

Coho salmon anti-*V. anguillarum* 775 serum with an agglutinin titer of 512 against the homologous bacterium had a titer of 8 against *Vibrio* sp. 1669. Immunodiffusion also revealed differences between the two vibrios. In Figure 2, the inner precipitin lines demonstrate antigenic cross-reactivity (reaction of identity). An additional antigen unique to *V. anguillarum* 775 is demonstrated by the outer precipitin line which is not present in reactions with *Vibrio* sp. 1669.

After all detectable agglutinin activity against

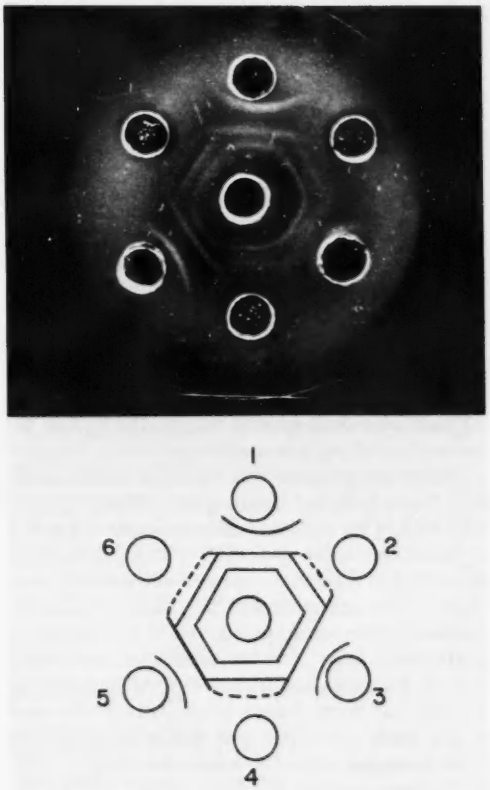

FIGURE 2. —Immunodiffusion comparison of *Vibrio anguillarum* 775 and *Vibrio* sp. 1669. Wells 1, 3, and 5 contain *V. anguillarum* 775 sonicate and wells 2, 4, and 6 contain *Vibrio* sp. 1669 sonicate. The center well contains rabbit anti-*V. anguillarum* 775 serum.

V. anguillarum 775 in rabbit anti-*Vibrio* sp. 1669 serum was removed by absorption, a titer of 16 against 1669 remained (Table 2), indicating that *Vibrio* sp. 1669 also contains antigenic determinants not present on *V. anguillarum* 775.

Whether a vaccine containing antigens from both vibrios would be more protective than vaccines containing antigens from only one of the vibrios is not known. This possibility is currently being investigated. Deoxyribonucleic acid homology experiments are also in progress to better clarify the taxonomic relation of the two vibrios.

TABLE 2. — Agglutinin titers of rabbit anti-*Vibrio* sp. 1669 serum unabsorbed and absorbed with *V. anguillarum* 775 antigen.

Condition	Titer	
	775	1669
Unabsorbed anti-1669 serum	8	32
Anti-1669 serum absorbed with 775	0	16

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RELATION OF FISH CATCHES IN GILL NETS TO FRONTAL PERIODS

A study was conducted in 1972 relating gill net catches of fishes to webbing material, time of day, and water depth in St. Andrew Bay, Fla. (Pristas and Trent[1]). While conducting the study, Pristas and Trent observed that catches in the nets appeared to be greater when atmospheric fronts moved through the area in the autumn. We decided to test the hypothesis that catches of fishes in gill nets increase during frontal periods. Experimental data were collected in September-December 1973, and the results of the analysis are presented in this paper.

[1]Pristas, P. J., and L. Trent. 1974. Comparisons of catches of fishes in gill nets in relation to webbing material, time of day, and water depth in St. Andrew Bay, Florida. Unpubl. manuscr.

Study Area and Methods

The study area was located about 300-800 m northwest of Courtney Point in St. Andrew Bay (Figure 1). Hydrological, physical, and sedimentological characteristics of the bay system were described by Ichiye and Jones (1961), Waller (1961), and Hopkins (1966). The bay system exchanges water with the Gulf of Mexico through East and West passes (Figure 1). Prevailing winds are from the southwest in the summer, north and northeast in the autumn, and north and southeast in the winter and spring. Tides are usually diurnal with a mean range of about 0.4 m in St. Andrew Bay (U.S. Department of Commerce 1967).

Eleven gill nets of different mesh sizes were fished for 87 consecutive days from 17 September to 13 December 1973. Each net was 33.3 m long and 3.3 m deep. Stretched mesh sizes ranged from 6.4 to 12.7 cm, the mesh sizes increasing by 0.6-cm increments. The nets were made of #208 monofilament nylon webbing hung to the float and lead lines on the half basis (two lengths of stretched mesh to one length of float line).

Nets were set parallel to each other about 50 m apart, perpendicular to shore, and in water depths (mean low tide) of 2.2 to 2.6 m (Figure 1). Nets remained in the water continuously except for 12 brief periods when they were randomly reset among net locations during the 87-day period. Damaged webbing never exceeded 5% of the total surface area of each net.

Fishes were removed from the nets at sunrise ±2 h and occasionally at sunset ±1 h. The total number of each species caught, including the damaged specimens, was counted. Lengths of the undamaged specimens were determined on a measuring board to the nearest 0.5 cm in fork length (tip of snout to fork of tail) for those fishes having forked tails and in total length (tip of snout to extremity of caudal fin) for Atlantic croaker and sharks.

Total catch and catches of each of the 10 most abundant species per 24-h period (catches per day) during and between frontal periods were compared using a t-test for unpaired observations (Steel and Torrie 1960). We tested the hypothesis that the mean catch during frontal periods (n = 23) equaled the mean catch between frontal periods (n = 64). We also used the t-test to test the hypothesis that the mean lengths of each of the 10 most abundant species caught during and between frontal periods were equal.

Water temperature was recorded continuously by a Peabody-Ryan[2] thermograph (Model F; accurate within 2% on time and temperature) about 1 m below the water surface at a dockside location about 100 m from the south end of the study area. Mean water temperatures per 24-h period were computed from readings taken every 6 h from the continuous data. Air temperatures, measured hourly, were obtained from the weather station at Tyndall Air Force Base located about 13 km east of the study area. Air and water temperatures were averaged over a 24-h period ending at 0600 h. Changes in water temperature per 24-h period were determined from these means.

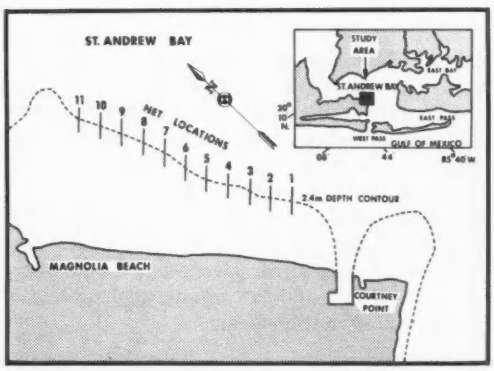

FIGURE 1.—Study area and net locations in St. Andrew Bay, Fla.

Species and Numbers of Fish Caught

A total of 15,398 individuals representing at least 65 species (not all species of *Sphyrna* and none of *Scorpaena* were specifically identified) of marine fishes was caught during the study (Table 1). Catch per day ranged from 10 to 967 individuals and from 6 to 25 species; increases and decreases in the total number of fish caught per day were generally accompanied by similar changes in the number of species of fish caught per day (Figure 2).

The 10 most abundant species comprised 88% of the total catch. The 10 were: Gulf menhaden, *Brevoortia patronus*; spot, *Leiostomus xanthurus*; Atlantic croaker, *Micropogon undulatus*; pinfish, *Lagodon rhomboides*; pigfish, *Orthopristis*

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Species and numbers of fish caught in gill nets during September-December 1973 in St. Andrew Bay, Fla.

Species	Number caught
Gulf menhaden, *Brevoortia patronus*	3,467
Spot, *Leiostomus xanthurus*	2,504
Atlantic croaker, *Micropogon undulatus*	2,335
Pinfish, *Lagodon rhomboides*	1,661
Pigfish, *Orthopristis chrysoptera*	905
Sea catfish, *Arius felis*	853
Bluefish, *Pomatomus saltatrix*	594
Spanish mackerel, *Scomberomorus maculatus*	563
Yellowfin menhaden, *Brevoortia smithi*	473
Gafftopsail catfish, *Bagre marinus*	239
Crevalle jack, *Caranx hippos*	212
Blue runner, *Caranx crysos*	211
Little tunny, *Euthynnus alletteratus*	170
Inshore lizardfish, *Synodus foetens*	123
Atlantic sharpnose shark, *Rhizoprionodon terraenovae*	94
Bonnethead, *Sphyrna tiburo*	91
Gulf flounder, *Paralichthys albigutta*	89
Florida pompano, *Trachinotus carolinus*	86
Atlantic bumper, *Chloroscombrus chrysurus*	78
Ladyfish, *Elops saurus*	74
Cobia, *Rachycentron canadum*	46
Blacktip shark, *Carcharhinus limbatus*	40
Blacknose shark, *Carcharhinus acronotus*	39
Harvestfish, *Peprilus alepidotus*	34
Yellow jack, *Caranx bartholomaei*	34
Remora, *Remora remora*	32
Hybrid menhaden, *Brevoortia smithi* × *patronus*	29
Sand seatrout, *Cynoscion arenarius*	29
Skipjack herring, *Alosa chrysochloris*	28
Bighead searobin, *Prionotus tribulus*	22
Spotted seatrout, *Cynoscion nebulosus*	22
Striped mullet, *Mugil cephalus*	22
Leatherjacket, *Oligoplites saurus*	22
Atlantic thread herring, *Opisthonema oglinum*	17
Longnose gar, *Lepisosteus osseus*	16
Florida smoothhound, *Mustelus norrisi*	15
Black drum, *Pogonias cromis*	12
Alabama shad, *Alosa alabamae*	11
Gray snapper, *Lutjanus griseus*	10
Atlantic spadefish, *Chaetodipterus faber*	10
Southern sea bass, *Centropristis melana*	8
Atlantic threadfin, *Polydactylus octonemus*	7
Finetooth shark, *Aprionodon isodon*	7
Sheepshead, *Archosargus probatocephalus*	6
Gulf toadfish, *Opsanus beta*	6
Orange filefish, *Aluterus schoepfi*	5
Gag, *Mycteroperca microlepis*	5
Sand perch, *Diplectrum formosum*	5
Atlantic moonfish, *Vomer setapinnis*	5
Hogchoker, *Trinectes maculatus*	4
White mullet, *Mugil curema*	4
Hammerhead shark, *Sphyrna* sp.	3
Southern stargazer, *Astroscopus y-graecum*	3
Smooth dogfish, *Mustelus canis*	3
Scorpionfish, *Scorpaena* sp.	2
Guaguanche, *Sphyraena guachancho*	2
Striped burrfish, *Chilomycterus schoepfi*	2
Dusky flounder, *Syacium papillosum*	2
Tarpon, *Megalops atlantica*	1
Bull shark, *Carcharhinus leucas*	1
Tripletail, *Lobotes surinamensis*	1
Shrimp eel, *Ophichthus gomesi*	1
Sandbar shark, *Carcharhinus milberti*	1
Bonefish, *Albula vulpes*	1
Halfbeak, *Hyporhamphus unifasciatus*	1
Total	15,398

chrysoptera; sea catfish, *Arius felis*; bluefish, *Pomatomus saltatrix*; Spanish mackerel, *Scomberomorus maculatus*; yellowfin menhaden, *Brevoortia smithi*; and gafftopsail catfish, *Bagre marinus* (Table 1). Catches per day of each of these are shown in Figure 3.

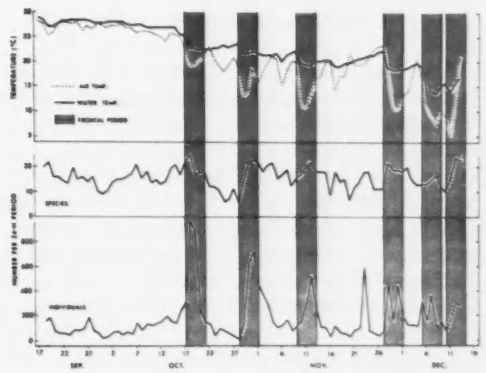

FIGURE 2.—Frontal periods, mean air and water temperatures, and numbers of species and individuals caught per 24-h period in St. Andrew Bay, Fla., September-December 1973.

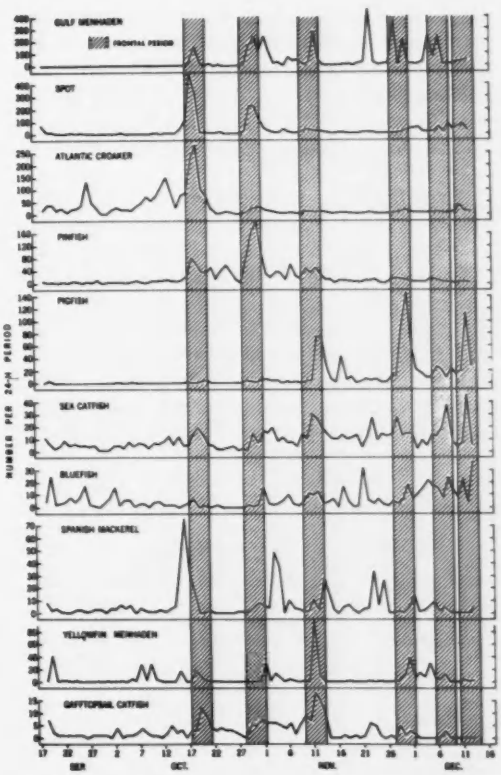

FIGURE 3.—Frontal periods and number of individuals caught by species per 24-h period in St. Andrew Bay, Fla., September-December 1973.

Frontal Periods

A frontal period was arbitrarily defined as any four consecutive days the first of which the water temperature dropped 2°C or more. Four days were selected, because fish catches were generally affected for 2 to 4 days following the initial temperature drop on the first day of a frontal period. Six frontal periods occurred in the study area from 17 September to 13 December (Figure 2). Fronts moved through the study area on 17 October, 28 October, 9 November, 27 November, 5 December, and 10 December (Figure 2). The average decrease of water and air temperatures per 24-h period for the above dates was 2.5°C and 6.4°C, respectively. In addition to decreases of temperatures, fronts passing through estuaries of the northern Gulf of Mexico are also characterized by: 1) rapid changes in barometric pressure, 2) shifts in wind direction and wind speed, 3) changes in tidal heights, and 4) increases in turbidity and velocity of tidal currents (E. J. Pullen, pers. commun., U.S. Corps of Engineers, Galveston, Tex.).

Catch Related to Frontal Periods

Each front was characterized by a marked increase in the numbers of individuals caught. Such a marked increase occurred only once (22-24 November) during a nonfrontal period (Figure 2). The mean number (all species combined) of fish caught per day was 354.7 during frontal periods and 113.1 between frontal periods (Table 2). Mean catches were significantly higher during frontal periods for all species combined and for 8 of the 10 most abundant species. Atlantic croaker and Spanish mackerel (Table 2, Figure 3) were the exceptions. Spanish mackerel was the only species caught in greatest numbers between frontal periods. Mean catches of the nine species ranged from 1.7 to 9.5 times greater during frontal periods than between frontal periods.

Mean lengths of fish caught during frontal periods were not significantly different from those caught between frontal periods for each of the 10 most abundant species (Table 2).

These results suggest that many species of marine fishes become more vulnerable to capture by gill nets in shallow areas of coastal bays during frontal periods in autumn. This increased vulnerability probably results from increased activity, migration, a lessening ability to avoid the net, and one or more of the factors associated with fronts, e.g., changes in temperature, tidal height, turbidity, and current velocity.

Acknowledgments

Our sincere appreciation is extended to J. R. Lara for furnishing climatological data and to D. B. Jester, M. A. Roessler, and J. Y. Christmas for their helpful comments.

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TABLE 2.—Comparisons of mean catches per day and mean lengths during and between frontal periods, September-December 1973, St. Andrew Bay, Fla.

Species group or species	Mean number caught per day			Mean length (cm)		
	During frontal periods	Between frontal periods	*t*-value	During frontal periods	Between frontal periods	*t*-value
All fish	354.7	113.1	−6.60**	[1]	[1]	[1]
Gulf menhaden	90.4	21.7	−3.46**	21.0	21.5	1.26
Spot	81.7	9.8	−4.66**	20.2	19.6	−1.85
Atlantic croaker	38.6	22.6	−1.43	26.2	25.6	−1.06
Pinfish	41.6	11.0	−4.46**	17.0	16.5	−0.64
Pigfish	30.4	3.2	−5.28**	18.2	18.9	1.36
Sea catfish	16.7	7.3	−5.68**	30.2	30.9	0.78
Bluefish	10.4	5.5	−2.74**	33.6	35.9	0.89
Spanish mackerel	5.0	7.0	0.70	34.9	36.9	1.15
Yellowfin menhaden	10.5	3.6	−2.22*	25.8	26.0	0.65
Gafftopsail catfish	5.0	2.0	−3.98**	42.7	44.2	1.06

[1]Not determined.
*Significant at 5% level.
**Significant at 1% level.

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PHOSPHOGLUCOMUTASE POLYMORPHISM IN TWO PENAEID SHRIMPS, *PENAEUS BRASILIENSIS* AND *PENAEUS AZTECUS SUBTILIS*

In a search for subpopulation differences within species of penaeid shrimp in the northern Gulf of Mexico, Proctor et al. (1974) and Marvin and Caillouet (1976) reported genetically controlled polymorphism in the enzyme phosphoglucomutase (PGM) in *Penaeus aztecus* (brown shrimp) and *P. setiferus* (white shrimp). The brown shrimp were collected in the northern Gulf of Mexico, so they are *P. aztecus aztecus* Ives, according to Pérez Farfante (1969). The white shrimp, collected both from the northern Gulf and from the North Edisto River, S.C., are *P. setiferus* (Linnaeus), according to Pérez Farfante (1969). Our paper describes similar polymorphisms in PGM in two more penaeids, *P. brasiliensis* Latreille and *P. aztecus subtilis* Pérez Farfante.

Methods

Specimens were collected off the coasts of Guyana, Surinam, and French Guiana, South America, on cruise 49 of the *Oregon II*, between lat. 6°13′ and 6°29′N and between long. 53°10′ and 53°36′W, at 22-29 fathoms, on 9 and 10 February 1974. They were stored at −20°C or below until analyzed. Preparation of abdominal muscle extracts, electropherograms of general protein patterns, and PGM zymograms followed procedures used by Procter et al. (1974). Each specimen was identified to species by morphological characteristics, then their distinctive general protein patterns (Figure 1) were used to confirm this identification. To do so, each gel was sliced horizontally into two halves after electrophoresis was complete. One half was treated with PGM specific stain and the other half was stained with Coomassie Blue.[1] Specimens of *P. aztecus aztecus*

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

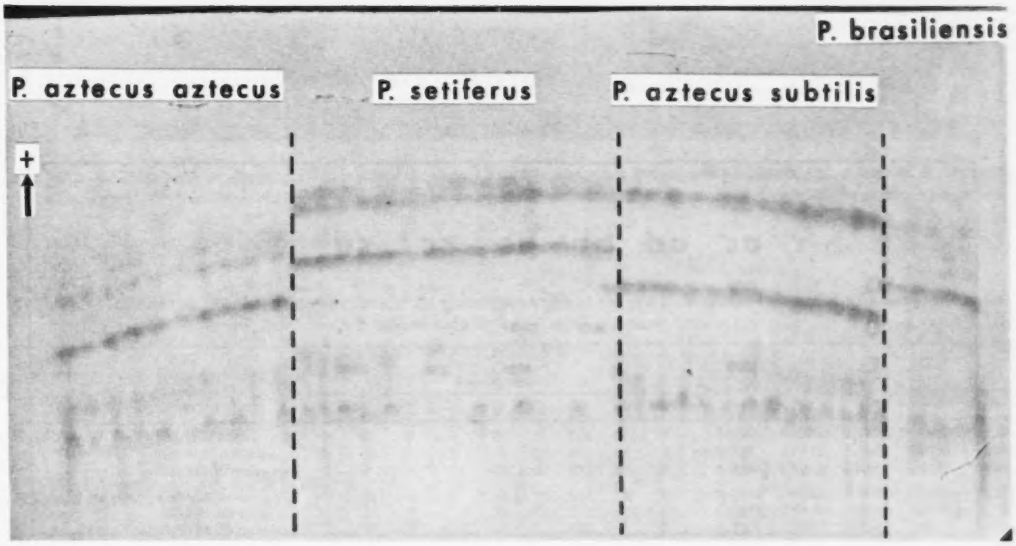

FIGURE 1. — Electropherogram showing general protein pattern of *Penaeus brasiliensis*, *P. aztecus subtilis*, *P. aztecus aztecus*, and *P. setiferus*. Stain used was Coomassie Blue. Direction (↑) of protein migration toward the anode (+) is shown.

and *P. setiferus* collected in the northern Gulf were included for comparison with *P. aztecus subtilis* and *P. brasiliensis*.

Results and Discussion

In *P. aztecus subtilis* the zymograms of abdominal muscle extracts exhibited a single region of PGM activity composed of five anodal bands which are labelled a, b, c, d, and e. The same was true for *P. brasiliensis* with the exception that band e was not observed. Bands a, b, c, and d are shown in Figure 2 and bands b, c, and d in Figure 3. Band e, observed in *P. aztecus subtilis*, is shown only diagrammatically (Figure 3). Direct comparison of PGM bands among *P. brasiliensis*, *P. aztecus subtilis*, *P. aztecus aztecus*, and *P. setiferus* suggested that bands b, c, and d are similar in these shrimps (Figure 4). This result is supported by Marvin and Caillouet (1976) who showed that *P. setiferus* and *P. aztecus aztecus* have the same five PGM bands. These bands are assumed to be under the control of five codominant allelic genes designated PGM_a through PGM_e (Proctor et al. 1974; Marvin and Caillouet 1976).

Six phenotypes of PGM were observed in *P. brasiliensis* and eight in *P. aztecus subtilis* (Table 1). PGM phenotypes were enumerated from zymograms to determine numerical distributions of phenotypes, and allele (PGM band) frequencies were derived therefrom (Table 1). Two-banded phenotypes (Figures 2-4) observed in some individuals presumably reflect heterozygous individuals. With PGM phenotypes grouped into three categories, cc, cx, and xx (where x includes bands a, b, d, and e), chi-square tests detected no difference ($P>0.05$) in phenotype distribution between the sexes in either species. With the same

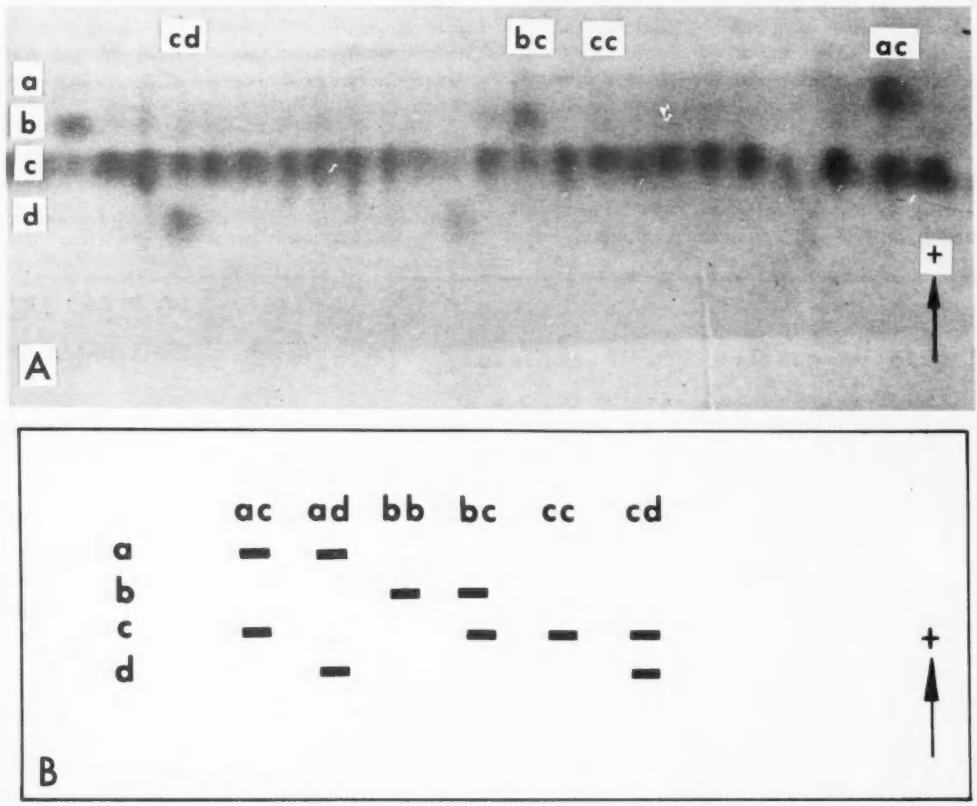

FIGURE 2. — A. Zymogram showing PGM bands a through d (band e not shown) and phenotypes cd, bc, cc, and ac. B. Diagram showing six PGM phenotypes observed in *Penaeus brasiliensis*. Direction (↑) of protein migration toward the anode (+) is shown.

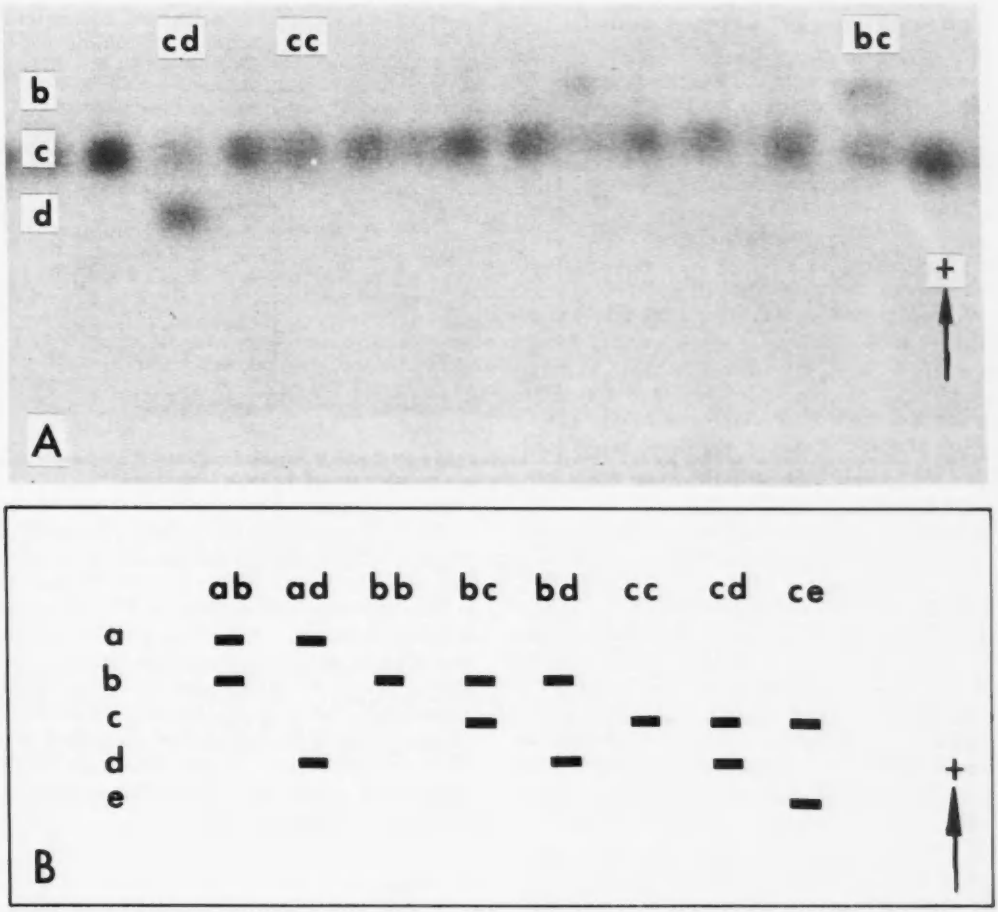

FIGURE 3. — A. Zymogram showing PGM bands b through d (bands a and e not shown) and phenotypes cd, cc and bc. B. Diagram showing eight PGM phenotypes observed in *Penaeus aztecus subtilis*. Direction (↑) of protein migration toward the anode (+) is shown.

TABLE 1. — Distribution (number of specimens) of PGM phenotypes and frequency of PGM alleles in samples of *Penaeus brasiliensis*, *P. aztecus subtilis*, and *P. aztecus aztecus*.

Species	Total length[1] range (mm)	Sex	Phenotypes									Alleles				
			ab	ac	ad	bb	bc	bd	cc	cd	ce	a	b	c	d	e
P. brasiliensis	145-185	Male	0	2	0	1	12	0	172	17	0	0.0049	0.0343	0.9191	0.0417	0.0000
	151-210	Female	0	2	1	0	8	0	161	14	0	0.0081	0.0215	0.9301	0.0403	0.0000
	145-210	Combined	0	4	1	1	20	0	333	31	0	0.0064	0.0282	0.9244	0.0410	0.0000
P. aztecus subtilis	102-152	Male	0	0	2	0	13	2	143	6	0	0.0060	0.0452	0.9187	0.0301	0.0000
	107-175	Female	1	0	0	1	13	0	119	8	2	0.0035	0.0556	0.9062	0.0278	0.0069
	102-175	Combined	1	0	2	1	26	2	262	14	2	0.0048	0.0500	0.9129	0.0290	0.0032
P. aztecus aztecus[2]	60-100	Combined	1	2	0	22	211	5	345	12	2	0.0025	0.2175	0.7642	0.0142	0.0017

[1]Tip of rostrum to tip of telson.
[2]Data adapted from Proctor et al. (1974).

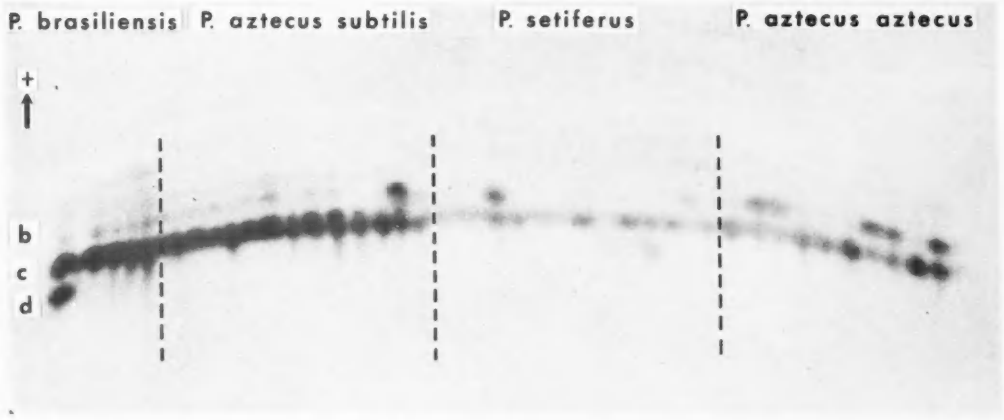

FIGURE 4.—Zymogram comparing PGM bands b through d (bands a and e not shown) in *Penaeus brasiliensis, P. aztecus subtilis, P. aztecus aztecus*, and *P. setiferus*. Direction (↑) of protein migration toward the anode (+) is shown.

phenotype categories, but with data for sexes combined, the phenotype distribution of *P. aztecus subtilis* deviated significantly ($\chi^2 = 7.086$, $0.025<P<0.05$) from that expected from Hardy-Weinberg equilibrium (Stern 1943). The reason for this deviation is not known. Johnson et al. (1974) noted a deviation from Hardy-Weinberg expectation for PGM phenotype distribution of a pandalid shrimp *Pandalus hypsinotus* Brandt, in Alaska, and they suggested that it might be related to depth of capture as found in, Pacific ocean perch, *Sebastodes alutus* (Johnson et al. 1971).

Our study provided an opportunity to compare the subspecies *P. aztecus subtilis* and *P. aztecus aztecus,* therefore distribution of PGM phenotypes and frequency of PGM alleles for the latter subspecies (data adapted from Proctor et al. 1974) also are shown in Table 1. This comparison is based on the assumption that bands a and e as well as bands b, c, and d are similar in the two species. However, even if this is not the case, the small frequencies of the rare a and e alleles would not appreciably affect the comparison. Both subspecies exhibited eight phenotypes, but not all were the same. Phenotype ad was detected in *P. aztecus subtilis* but not in *P. aztecus aztecus*. Phenotype ac was detected in the latter but not in the former. With phenotypes grouped into categories cc, cx, and xx, and with sexes combined, a chi-square contingency test detected a significant ($P<0.05$) difference in phenotype distribution between the subspecies, and this result provides an additional characteristic to existing evidence of differences between these subspecies (see Pérez Farfante 1969).

This and previous studies by Proctor et al. (1974) and Marvin and Caillouet (1976) suggest that zymogram analysis may provide a useful tool in the study of population genetics of the Penaeidae. The wide distribution (Mistakidis 1968), commercial importance, and relatively short generation time of the Penaeidae should make them particularly attractive subjects of study by population geneticists.

Acknowledgments

Through initial efforts by Raphael R. Proctor, Jr., Gulf Coastal Fisheries Center, National Marine Fisheries Service (NMFS), Galveston, Tex., this study was made possible. His helpful suggestions were greatly appreciated. We are grateful to Albert C. Jones, Alexander Dragovich, and Donald M. Allen, Southeast Fisheries Center, NMFS, Miami, Fl., for providing specimens for this study. Fred M. Utter, Northwest Fisheries Center, NMFS, Seattle, Wash., reviewed the manuscript. Frank Patella conducted the statistical analyses for the study.

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FIRST RECORD OF THE MELON-HEADED WHALE, *PEPONOCEPHALA ELECTRA*, IN THE EASTERN PACIFIC, WITH A SUMMARY OF WORLD DISTRIBUTION

Peponocephala electra (Gray 1846) is a tropical pelagic delphinid previously known to occur in the eastern Atlantic, Indian, and western and central Pacific oceans. It is also known as the electra dolphin, the Hawaiian blackfish, and the many-toothed blackfish. Since van Bree and Cadenat (1968; localities 1-4, 6-9, 11, 13, 14, 16, 18, and 19 in Figure 1) summarized world records, the species has been reported from Thailand (Pilleri 1973, locality 17), the Philippine Sea near Cebu (W. H. Dawbin pers. commun., locality 15), near Townsville, Australia (G. E. Heinsohn pers. commun., locality 12), the New Hebrides (Rancurel 1974, locality 10), and the Tuamotos-Marquesas region (K. S. Norris pers. commun., locality 5). Records cited by van Bree and Cadenat (1968) as "in litteris" or in press, have subsequently been published (Dawbin et al. 1970, locality 11; Mörzer Bruyns 1971, localities 6-9). The purpose of this note is to report a capture that extends the known range of the species some 3,000 miles into the eastern tropical Pacific off Central America (Figure 1; triangle).

The specimen (Figure 2), a male calf 112 cm long (tip of upper jaw to base of notch in flukes) and weighing 15 kg, was captured in a tuna purse seine that had been set on an aggregation of yellowfin tuna, *Thunnus albacares*, and dolphins, *Stenella* sp., approximately 90 nautical miles (about 167 km) due west of Champerico, Guatemala (lat. 14°20'N, long. 91°52'W), in May 1974. More precise information on date and locality of capture is not available. A crew member found the calf dead in the net, placed it in the ship's freezer, and on return to port donated it to the National Marine Fisheries Service, La Jolla. The specimen was identified using X rays of the dentition. The high tooth count ($\frac{23+|23+}{22+|22+}$), combined with the blunt head and dark coloration, is diagnostic of the species. The specimen was then photographed, measured, weighed, cast in plastic, and sent frozen to the U.S. National Museum (USNM), Washington, D.C., where it was preserved whole

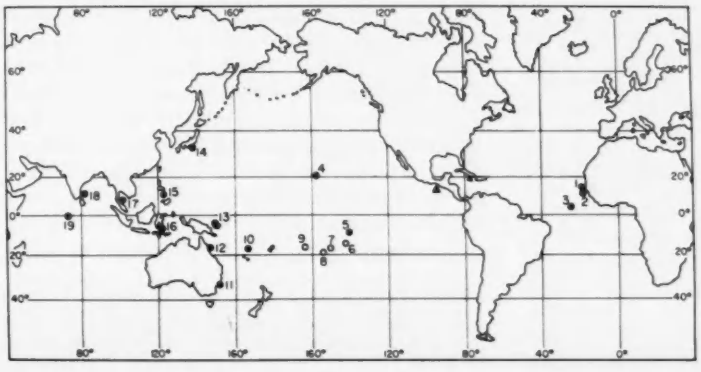

FIGURE 1. — Known distribution of *Peponocephala electra*. Triangle is new record; sources of others in text. Closed circles are specimen localities, open circles are sightings. Some circles represent multiple records from single localities, e.g., Hawaii and Honshu, Japan.

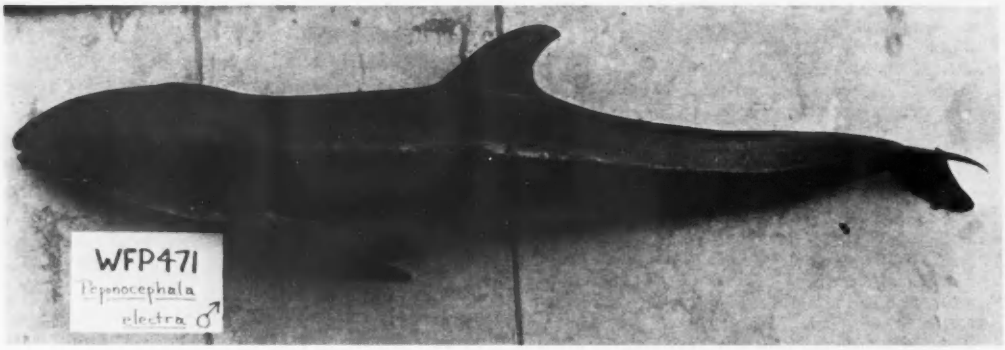

FIGURE 2. — Calf of *Peponocephala electra* collected in eastern tropical Pacific (USNM 504087).

and placed in the marine mammal collection (USNM 504087).

Acknowledgments

I thank Edward Kovalchek and Joseph Madruga for providing the specimen and P. J. H. van Bree for reading the manuscript.

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FOODS OF JUVENILE SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, IN THE INSHORE COASTAL WATERS OF BRISTOL BAY, ALASKA, 1966-67

For most living organisms the early portion of life is most critical in determining survival. Anadromous fishes such as Pacific salmon have two critical periods during early life — development and growth in fresh water and subsequent adaptation to a marine environment. The food of juvenile salmon during the first few months of marine life influences growth and condition, which in turn probably influences parasitism, predation, and other factors which ultimately determine marine survival.

Although the sockeye salmon, *Oncorhynchus nerka* (Walbaum), is one of the most valuable commercial fishes in Alaska and has been the object of extensive research, little is known of its early life in the sea. Straty (1974) and Straty and Jaenicke[1] have made the only comprehensive study of early marine life of the sockeye salmon in Bristol Bay, historically the largest sockeye fishery in the North Pacific. Documented studies of sockeye salmon food habits during this period of life are generally limited to brief accounts of Soviet research in Kamchatka waters (Synkova 1951), a study in British Columbia (Manzer 1969), examination of a few specimens from Aleutian and Kodiak waters (Chamberlain 1907), and 45 specimens taken off Cape Seniavin in lower

[1]Straty, R. R., and H. W. Jaenicke. 1971. Studies of the estuarine and early marine life history of sockeye salmon in Bristol Bay, 1965-67. Unpubl. manuscr., 137 p. Northwest Fish. Cent. Auke Bay Lab., Natl. Mar. Fish. Serv., NOAA, Auke Bay, AK 99821.

Bristol Bay (Dell 1963). Recently, Jaenicke and Bonnett[2] completed an extensive study of the foods of some 1,200 seaward-migrating sockeye salmon in Bristol Bay during 1969 and 1970. Most of their samples were taken over deeper waters farther offshore than mine — particularly those off Port Moller.

The purpose of my study was to document the foods of seaward-migrating sockeye salmon along the main migration route on the north side of the Alaska Peninsula in Bristol Bay, Alaska, during 1966 and 1967. Later studies by Straty and Jaenicke (see footnote 1) and Jaenicke and Bonnett (see footnote 2) show that the areas where I took samples of juvenile sockeye salmon (Kvichak to Port Moller — Figure 1) were indeed along the main migration route in the upper and central parts of the bay (Kvichak to Port Heiden). In lower Bristol Bay, however, my sampling area (Port Moller) was inshore from the usual main migration route. In years when unusually cold seawater temperatures prevail, the main migration route in the lower bay shifts to the warmer inshore waters (Straty 1974). The juvenile sockeye salmon I sampled in the Port Moller area were taken in a year (1967) when normal temperatures prevailed and were presumably inshore from the path followed by most migrants that year. However, the foods found in 1967 in these inshore waters may reflect what is usually available to the main body of outmigrants in colder years when their path is altered.

[2]Jaenicke, H. W., and M. B. Bonnett. Food of sockeye salmon outmigrants in Bristol Bay, Alaska, 1969-70. Unpubl. manuscr., 20 p. Northwest Fish. Cent. Auke Bay Lab., Natl. Mar. Fish. Serv., NOAA, Auke Bay, AK 99821.

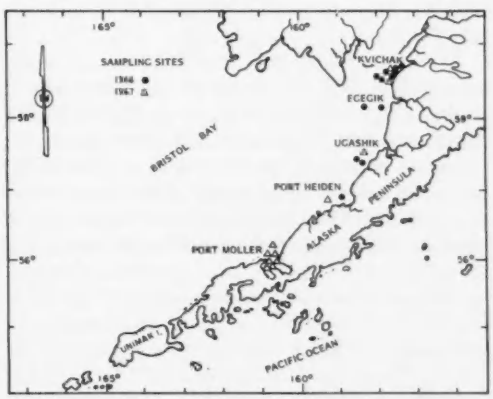

FIGURE 1. — Bristol Bay, Alaska, showing locations where juvenile sockeye salmon were collected in 1966 and 1967 for food habit analyses. Samples in the upper bay (Kvichak and Egegik) were taken in June, and those in the central bay (Ugashik) and lower bay (Port Heiden and Port Moller) were taken from July to September.

Materials and Methods

The samples of juvenile sockeye salmon were collected in 1966 and 1967 in the following areas (Figure 1) and times: Kvichak, June of both years; Egegik, June 1966; Ugashik, July and September 1966 and August 1967; Port Heiden, July 1966 and August 1967; and Port Moller, July and August 1967. All samples were taken during daylight, usually between 1000 and 1900 h.

In 1966, the juvenile sockeye salmon were collected with circular tow nets (2.1 m in diameter) and a small-mesh round haul seine (110 m long by about 7 m deep); in 1967 they were collected in a small-mesh lampara seine (183 m long by about 14 m deep). All sampling was done from the 13-m National Marine Fisheries Service vessel *Sockeye*. Samples were preserved in 10% Formalin[3] solution and processed later.

I analyzed the stomach contents of 160 juvenile sockeye salmon and all but 16 contained food. These 160 fish represented roughly equal numbers of individuals from 1-cm size groups ranging from 6- to 13-cm fork length and were from all five areas of Bristol Bay from Kvichak Bay south to Port Moller — a distance of about 320 km.

The stomach (that portion of the digestive tract from the anterior end of the esophagus to the pylorus) of each specimen was removed, and all food organisms were separated and identified to the lowest taxonomic level practical. All of the food items were air dried overnight at room temperature and weighed to the nearest 0.1 mg the following day.

The eight major categories of food items: copepods, fish, larval crustaceans, euphausiids, amphipods, insects, miscellaneous crustaceans, and zoofauna, are not mutually exclusive. The least specific categories merely reflect the digested condition or incidental importance of a given item, e.g., crustacean remains (recorded as miscellaneous crustaceans) or arachnids (zoofauna), which occurred only once.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

For each sampling area, the weight of each major food category was calculated as the percentage of the total dry weight of all food found. The percentage of occurrences and weights of foods were based only on those specimens containing food.

Results

The foods consumed by seaward-migrating sockeye salmon in Bristol Bay varied in the relative proportion and occurrence of kinds and quantities between months during the summer. The apparent differences between the upper and lower areas of the bay are largely due to date of sampling. The 16 empty stomachs found were collected in June from the upper bay — the Kvichak and Egegik areas.

In early June 1966 in the Kvichak area, 11 of 19 juvenile sockeye salmon contained food. Although fish and insects made up 97% of the bulk (weight), fish occurred in only 5% of the stomachs and insects in 53%. By late June in the same area, 8 of 10 stomachs contained food, most of which was copepods. They made up 89% of the bulk and were found in 70% of the stomachs; miscellaneous crustaceans were found in 60%. In mid-June of the following year (1967), 18 of 21 juvenile sockeye salmon from the Kvichak area contained food. Fish, insects, and copepods made up 93% of the bulk; fish occurred in 19% of the stomachs, insects in 76%, and copepods in 62%.

In mid-June 1966, 20 of 23 stomachs collected farther seaward at Egegik contained very small amounts of food. Euphausiids and miscellaneous crustaceans made up 78% of the bulk, but euphausiids occurred in only 9% of the stomachs and miscellaneous crustaceans in 13%. Insects occurred in 48% of the stomachs, but made up only 4% of the bulk.

In mid-July 1966 at Ugashik, all 20 stomachs collected contained larval crustaceans (79% by bulk and mostly anomurans). Copepods were insignificant in terms of bulk but occurred in 70% of the stomachs. At Port Heiden (farther seaward) on the same date, fish made up 76% of the bulk of the contents of the seven stomachs collected. Fish occurred in 28% of the stomachs, whereas amphipods occurred in 71% and insects in 57%.

At Port Moller in lower Bristol Bay throughout July and on 1 August 1967, copepods made up 71% of the bulk of food in 48 stomachs and occurred in 85%; larval crustaceans occurred in 58%, amphipods in 50%, and fish in 42%.

By mid-August 1967, when most juvenile sockeye salmon have migrated out of Bristol Bay (Straty 1974), the two juveniles taken at Ugashik contained only copepods and insects and two taken at Port Heiden contained mostly fish.

Only eight juvenile sockeye salmon were taken in September 1966 in the Ugashik area. Copepods and fish accounted for 86% of the stomach contents, but only copepods occurred frequently (100% with copepods vs. 25% with fish).

As the young sockeye salmon migrated seaward over successive months, they ate increasing amounts of food. In the Kvichak and Egegik areas during June, 16 of the 73 stomachs examined were empty and the others had only relatively small amounts of food (average of 3-6 mg). Later in the summer and farther at sea (Ugashik and Port Heiden) the average amount of food per stomach was much greater (20-24 mg), and still later in the summer and farther at sea (Port Moller), the amounts were the highest of all (average of 82 mg).

In terms of both bulk and frequency of occurrence, copepods were the most important food of juvenile sockeye salmon in inshore Bristol Bay in 1966 and 1967 (Tables 1, 2). Two genera of calanoid copepods (*Eurytemora* and *Metridia*) made up 98% of the number of copepods in the stomachs of 50 juveniles taken by Straty and Jaenicke (see footnote 1) in 1967 at Kvichak and

TABLE 1.—Percentage total dry weight of foods consumed by juvenile sockeye salmon collected at five areas in Bristol Bay, Alaska, 1966 and 1967.

Food category	Kvichak $N = 50$	Egegik $N = 23$	Ugashik $N = 30$	Port Heiden $N = 9$	Port Moller $N = 48$
Copepods	30.3	8.6	25.4	6.3	71.2
Fish	45.7	4.1	22.6	80.3	11.8
Larval crustaceans	0.1	0.4	44.6	—	5.7
Euphausiids	—	43.1	0.4	—	5.2
Amphipods	0.6	1.0	1.3	4.8	4.7
Insects	18.6	3.9	0.9	0.7	0.8
Miscellaneous crustaceans	2.6	34.9	0.2	0.1	0.5
Zoofauna	2.1	3.3	4.7	6.1	0.2
Other	—	0.8	—	1.8	—

TABLE 2. — Summary of foods eaten by juvenile sockeye salmon (N = 160) in all regions of Bristol Bay, Alaska, between June and September 1966 and 1967.

Food category	Percentage total dry weight	Percentage occurrence
Copepods	60.4	66.7
Fish	17.4	25.0
Larval crustaceans	9.8	35.4
Euphausiids	4.6	6.3
Amphipods	4.0	29.2
Insects	1.6	41.0
Miscellaneous crustaceans	0.9	22.2
Zoofauna	1.1	18.8
Other	0.1	2.8
Empty stomachs	—	10.0

Port Moller. (The 50 specimens were taken at the same time and place as my samples.) Fish were second in importance to copepods in terms of weight of food, and over half the bulk of these fish were Pacific sand lance, *Ammodytes hexapterus*. Larval crustaceans were the only other food of major importance (by bulk) and most of these were anomuran larvae eaten by juveniles in the Ugashik area in July 1966. Other items eaten by juvenile sockeye salmon in significant amounts during their migration out of Bristol Bay were euphausiids, amphipods, and insects. Insects and amphipods occurred frequently in the diet but did not contribute much bulk.

I looked for differences in food selectivity between large and small fish among 144 juveniles (6-13 cm fork length) grouped in 1-cm size categories, but the results were inconclusive.

Discussion

The results of this study generally agree with those of other investigators. The importance of copepods in the diet of juvenile sockeye salmon near shore in Bristol Bay is paralleled in coastal waters of British Columbia (Manzer 1969) and is similar to Kamchatka coasts, where copepods and cladocerans were the predominant foods of juvenile sockeye salmon (Synkova 1951). My findings differ from those of Jaenicke and Bonnett (see footnote 2), who sampled mainly over deeper waters of Bristol Bay farther offshore than I did, and Dell (1963), who sampled off Port Moller in Bristol Bay. Jaenicke and Bonnett examined the food of over 1,200 juvenile sockeye salmon captured during the summers of 1969-70 and found that the main items (in bulk) were young and larval sand lance and euphausiids. Similarly, Dell reported that 45 juvenile sockeye salmon taken in late July 1962 contained mostly larval sand lance and euphausiids.

Nearly all of the insects I found were from juvenile sockeye salmon captured in the Kvichak and Egegik areas in June (Table 1). These areas are contiguous to many rivers that form part of a major sockeye salmon reproductive complex of lakes and steams (Figure 1). According to Hartman et al. (1967), most of the migration from freshwater to Bristol Bay takes place in June. Most of the insects were probably ingested in fresh water when the fish were migrating seaward, suggesting that many of the juveniles taken in these areas were recent immigrants from fresh water. The occurrence of the only empty stomachs and small average weight of food per fish at Kvichak and Egegik suggest that the juveniles eat very little when they first enter salt water. Straty (1974) concluded that the young sockeye salmon did not feed when they entered Bristol Bay or that food was scarce. Reduction of feeding could be caused by a number of factors other than lack of food, including the physiological strain of adjusting osmoregulatory function from a freshwater to a marine environment.

The differences I observed in the types, relative proportions, and amounts of food eaten over successive months by the juvenile sockeye salmon as they progressed seaward can be largely attributed to food availability. Near-surface waters in the Kvichak area contained an average of 27 zooplankters per cubic meter in June, while near Port Moller in July the density was 1,400-8,100 (see footnote 1). Straty (1974) compared zooplankton abundance in the inner part of Bristol Bay (above Port Heiden) and the outer part (below Port Heiden) during 1969-71 and concluded that zooplankton was much more abundant as one progressed seaward.

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OCCURRENCE OF TWO GALATHEID CRUSTACEANS, *MUNIDA FORCEPS* AND *MUNIDOPSIS BERMUDEZI*, IN THE CHESAPEAKE BIGHT OF THE WESTERN NORTH ATLANTIC OCEAN[1,2]

Living male specimens of *Munida forceps* A. Milne-Edwards and *Munidopsis bermudezi* Chace (Table 1) were collected on the continental slope and rise south of Norfolk Canyon off the coast of Virginia on 18-19 November 1974. An ovigerous female *M. bermudezi* was also collected on 14 September 1975 in the Norfolk Canyon. They were taken with a 15-m shrimp trawl (12-mm stretch mesh inner liner) towed from the RV *James M. Gillis* (University of Miami, Florida).

Munida forceps has been reported from 80 to 338 m within the Gulf of Mexico and in the southwestern Atlantic between lat. 22°46.5′ and 26°37.0′N (Chace 1940, 1942; Springer and Bullis 1956; Bullis and Thompson 1965). Our find is consistent with the previously reported depth range, but it extends the geographic range of the species northward by 10° latitude.

Munidopsis bermudezi has been reported from the coast of Cuba (lat. 21°19′N, long. 76°05′W) at a depth of 2,654 m (Chace 1940, 1942), the Gulf of Mexico (lat. 25°50.5′N, long. 94°27′W) at 3,294 m (Pequegnat and Pequegnat 1970), and north of the Azores (lat. 45°26′N, long. 25°45′W) at 3,171 m (Sivertsen and Holthuis 1956).

The *Munida forceps* sample also included the galatheids *M. iris* A. Milne-Edwards and *M. longipes* A. Milne-Edwards and other decapods including *Bathynectes superbus* (Costa), *Cancer borealis* Stimpson, *C. irroratus* Say, *Homarus americanus* H. Milne Edwards, and penaeidean and caridean shrimps. The association of *M. forceps* with *M. iris* and *M. longipes* in our sample is previously unreported. Some previous records have shown associations with *M. stimpsoni* A. Milne-Edwards (Chace 1942) and with *M. flinti* Benedict and *M. irrasa* A. Milne-Edwards (Milne-Edwards 1880 from Pequegnat and Pequegnat 1970). Others (Benedict 1902; Bullis and Thompson 1965; Pequegnat and Pequegnat 1970) have not specified association of *M. forceps* with other galatheids.

TABLE 1.—Station and morphometric data for *Munida forceps* and *Munidopsis bermudezi* captured near Norfolk Canyon off the coast of Virginia. Length and width measurements in millimeters.

Item	*Munida forceps*	*Munidopsis bermudezi*	
	Male	Male	Female
Station	79	86	35
Collection	C74-499	C74-506	C74-168
Location, lat.	36°43.2′N	36°41.6′N	36°57.9′N
long.	74°38.0′W	73°47.0′W	73°21.5′W
Date of collection	Nov. 1974	Nov. 1974	Sept. 1975
Depth (m)	220-310	2,620-2,650	2,915-2,955
Bottom temperature (°C)	10.6	3.0	2.3
Bottom salinity (‰)	—	34.82	35.11
Total length (rostral tip to posterior margin of telson)	34	81.4	83.2
Carapace width, anterior	7.9	28.4	28.8
posterior	10.4	31.0	31.5
Carapace length (orbit to posterior margin)	13.5	33.5	33.5
Carapace length (including rostrum)	18.5	44.8	43.8
Cheliped (right) length	45	42.4	40.8
Carpus length	4.0	8.5	7.5
Merus length	15.2	14.5	13.0
Propodus length	25.6	19.3	14.3
Propodus width	4.5	8.8	8.0
Dactylus length	15.1	10.5	8.3
Second left pereopod length	28.8	48.7	46.5

[1]Research supported by National Science Foundation Grant GA-37561, J. A. Musick, Principal Investigator and by U.S. Department of Commerce, National Marine Fisheries Service Contract No. 03-4-043-353 for C.E.L. and P.A.H. participation.
[2]Contribution No. 717, Virginia Institute of Marine Science.

In November 1974, *Munidopsis bermudezi* was associated with *M. curvirostra* Whiteaves. Previous accounts did not indicate association of *M. bermudezi* with other galatheids. Other decapods taken in the November sample were *Lithodes agassizii* Smith, *Stereomastis sculpta* (Smith), and penaeidean and caridean shrimps, including *Hymenodora gracilis* Smith, a species occurring in the Azores sample (Sivertsen and Holthuis 1956).

In September, *M. bermudezi* was associated with *M. bairdii* (Smith) and *M. crassa* (Smith), as well as *Lithodes agassizii* and caridean shrimp.

The ovigerous *M. bermudezi* had not shed all eggs onto the pleopods. The 19 external eggs were tan and averaged 2.8 mm in diameter. These eggs were spherical with no visible blastoderm and were recently extruded. The ovary was tan and very well developed. It contained 106 ova averaging 2.7 mm in diameter. All eggs were measured with an ocular micrometer.

We suspect that these species with tropical affinities are normally present, though rare, in the Chesapeake Bight; but they could be accidental migrants. In either case, the probability of detection was raised by the recent increase in sampling intensity in the vicinity of Norfolk Canyon as compared to other areas of the continental slope between Florida and North Carolina. The question of how far north the tropical fauna extends along the southeastern coast of North America is still unanswered (Briggs 1974). Cerame-Vivas and Gray (1966) noted that the inshore fauna of the North Carolina shelf was warm temperate (Carolinian) but that the offshore fauna was tropical. In a study of sea stars of North Carolina, Gray et al. (1968) found 13 species that occurred in a northward extension of the Caribbean Province along the outer shelf and that these species ranged slightly northward past Cape Hatteras.

The authors are grateful for the assistance of Fenner A. Chace Jr., in confirming the identification of the specimens. All specimens have been deposited at the United States National Museum, Washington, D.C.

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EFFECTS OF MERCURY, CADMIUM, AND LEAD SALTS ON REGENERATION AND ECDYSIS IN THE FIDDLER CRAB, *UCA PUGILATOR*

Crabs are capable of autotomizing injured limbs at a preformed breakage plane and subsequently regenerating them. The regenerating limb bud grows in a folded position within a layer of cuticle, and unfolds when the animal molts. The length of regenerating limb buds is generally expressed in terms of "R-value" (Bliss 1956) which is length of limb bud × 100/carapace width. Such a regeneration index is useful for comparisons of crabs of different sizes. Since regeneration always terminates with a molt, the presence of regenerating limbs can affect the timing of ecdysis, and factors which influence ecdysis will also affect regeneration. For example, removal of eyestalks, a source of molt-inhibiting hormones, is a standard way of inducing precocious molting. Such animals will regenerate missing limbs rapidly, but will generally die at ecdysis. Skinner and Graham (1972) have shown that multiple autotomy, producing many regenerating limb buds, can cause accelerated regeneration, also leading to precocious molt.

Heavy metals as pollutants of the marine environment are of great concern. These chemicals are released as a result of industrial processes and tend to be toxic and to accumulate in organisms. Their toxicity to Crustacea has been studied by Corner and Sparrow (1957), Wisely and Blick (1967), Eisler (1971), Vernberg and Vernberg (1972), and O'Hara (1973).

This paper reports on the effects of mercury, lead, and cadmium on regeneration in the fiddler crab, *Uca pugilator*. With its estuarine intertidal habitat, this crab is likely to be subject to heavy metal pollution in industrial areas.

Materials and Methods

Fiddler crabs were collected in July and August from Accabonac Harbor, near East Hampton, N.Y., and brought into the laboratory. Autotomy of one chela and six walking legs was induced by pinching each merus with a hemostat. Immediately after autotomy, crabs were placed in solutions of $Pb(NO_3)_2$ (Reagent grade, Fisher Scientific), $HgCl_2$ (Reagent grade, Fisher Scientific), or anhydrous $CdCl_2$ (Reagent grade, Matheson, Coleman and Bell) at concentrations of 0.1 or 1.0 mg/liter of the metal ion. Crabs were maintained in groups of 10 in 1-liter glass aquaria in 200 ml of filtered seawater (30‰ salinity, room temperature 25°C). Twice weekly the aquaria were washed out and redosed. (In a similar static experimental design, Jackim et al. (1970) determined that the loss of metal ion from solution over a 96-h period was 0% for cadmium, 26% for mercury, and 79% for lead.) Crabs were fed twice weekly with Purina Fly Chow[1]. In all experiments, groups were arranged to have the same mean carapace width and to have equivalent distribution of males and females (5/5).

The growth of limb buds was measured twice weekly under a dissecting microscope with a calibrated ocular micrometer. In all cases, the first walking leg was measured as a representative limb. Values thus obtained were converted to R-values, and the means for each group were compared by the use of the *t*-test. Times of molting were recorded for all animals. Limb buds reached R-values of about 20 just prior to ecdysis.

Whole crabs were analyzed for mercury, cadmium, and lead following 2 wk of exposure to 0.1 mg/liter. Five crabs were used for each assay, which was done by New Jersey Department of Health personnel, using atomic absorption spectrophotometry.

Results

In experiment 1, crabs (mean carapace width 15 mm, range 13-16 mm) were exposed to 0.1 mg/liter of lead, cadmium, and mercury. Ten crabs were in each group, total biomass about 11 g. Cadmium had a retarding effect on regeneration (Table 1) although most individuals had molted by 28 days. The majority of controls molted by 21 days, and the rest completed ecdysis by 24 days. Mercury and lead had no retarding effect.

This experiment was repeated with crabs of a somewhat smaller size (13 mm carapace width, range 11-14 mm). Although cadmium again retarded regeneration, the retardation was less and was not always statistically significant (Table 1). These crabs reached ecdysis at the same time as controls (21 days). No effects of lead or mercury were seen.

In experiment 2, crabs were exposed to lead, mercury, and cadmium at concentrations of 1.0 mg/liter. Carapace width of crabs was 15 mm

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—R-values (mean ± standard error) of first walking legs of crabs after multiple autotomy and treatment with Pb, Hg, and Cd at 0.1 mg/liter.

Chemical	Days				
	7	10	14	17	21
Carapace width 15 mm:					
Controls	1.8 ± 0.3	7.3 ± 0.6	12.0 ± 0.7	18.4 ± 0.8	60% molt
Pb	2.8 ± 0.5	10.2 ± 0.7	14.7 ± 1.1	20.1 ± 0.6	80% molt
Hg	2.3 ± 0.2	8.8 ± 1.2	13.8 ± 1.3	17.7 ± 0.8	70% molt
Cd	1.0 ± 3.3	3.3 ± 0.7*	8.6 ± 1.2*	11.0 ± 1.3*	13.5 ± 1.5
Carapace width 13 mm:					
Controls	4.8 ± 0.4	10.6 ± 1.0	17.7 ± 1.0	20.2 ± 0.7 40% molt	70% molt
Pb	4.2 ± 0.4	9.2 ± 0.9	17.7 ± 0.8	18.2 ± 0.9 50% molt	90% molt
Hg	3.9 ± 0.7	9.4 ± 0.9	16.2 ± 1.1	17.9 ± 0.5 30% molt	60% molt
Cd	3.5 ± 0.6	8.0 ± 1.0	14.2 ± 1.1*	17.0 ± 0.8* 0% molt	70% molt

*P = 0.05 or less.

(range 14-16 mm). At this concentration, cadmium retarded regeneration to an even greater extent. This concentration of mercury was usually toxic, and the data obtained were from four crabs which survived the duration of the experiment. Regeneration did not take place in these crabs (Table 2). The cadmium, however, was not toxic, and all crabs survived, the majority (60%) completing ecdysis by 28 days. There was no mortality in lead, cadmium, or clean water in any of the experiments. The majority of controls molted by 24 days. A second group of crabs (carapace width 13 mm, range 12-14 mm) was exposed to cadmium and mercury at 1.0 mg/liter. Lead was not used in this experiment. Because of the high mortality in mercury in the previous experiment, 20 crabs were exposed to mercury. By the 17th day, the number surviving in mercury was reduced to eight, the same percentage as survived the previous experiment. The amount of growth in these crabs, though slight, was nevertheless much greater than in the previous experiment. Likewise, the retardation in cadmium was not as striking as in the earlier experiment (Table 2). The majority of controls molted by 21 days, whereas the majority in cadmium molted by 28 days. After 2½ wk, the eight crabs remaining in mercury were transferred to clean water, which was then changed daily, but they did not show evidence of recovery within 4 wk after return to clean water, during which time no significant growth occurred.

Residue analysis revealed that the crabs exposed for 2 wk to 0.1 mg/liter of mercury had absorbed 0.026 ± 0.001 ppm; those exposed to 0.1 mg/liter of cadmium had absorbed 0.50 ± 0.10 ppm; and those exposed to 0.1 mg/liter of lead had absorbed 2.04 ± 0.55 ppm.

Discussion

Retardation of regeneration was a specific effect of cadmium at both 0.1 and 1.0 mg/liter. At 0.1

TABLE 2. — R-values (mean ± standard error) of first walking legs of crabs after multiple autotomy and treatment with Pb, Hg, and Cd at 1.0 mg/liter.

Chemical	Days					
	7	10	14	17	21	24
Carapace width 15 mm:						
Controls	4.2 ± 0.4	8.0 ± 0.6	13.1 ± 1.0	15.9 ± 0.9	18.1 ± 0.3	70% molt
Pb	2.8 ± 0.6	6.2 ± 0.7	11.4 ± 1.0	14.5 ± 1.2	17.6 ± 0.7	70% molt
Hg	0*	0*	0*	0*	0.01 ± 0.01*	0.01 ± 0.01*
Cd	0.3 ± 0.2*	2.2 ± 0.8*	4.3 ± 1.2*	5.6 ± 1.5*	8.3 ± 2.5*	7.6 ± 2.3* 20% molt
Carapace width 13 mm:						
Controls	4.6 ± 0.5	10.2 ± 0.7	15.7 ± 0.9	18.0 ± 0.6	70% molt	90% molt
Hg	1.0 ± 0.6*	1.5 ± 0.8*	1.6 ± 0.8*	[1]2.1 ± 1.0*	2.7 ± 1.1*	2.9 ± 1.1*
Cd	3.5 ± 0.2	6.8 ± 0.6*	11.5 ± 1.3*	13.8 ± 1.5*	16.0 ± 2.0*	50% molt

[1]Returned to clean water.
*P = 0.05 or less.

mg/liter, mercury was not toxic and did not have an effect on the growth of limb buds. At 1.0 mg/liter, mercury caused almost total inhibition of limb growth, but also proved lethal to 60% of the crabs. Therefore, the inhibition of regeneration may not be a specific effect of the mercury, but just an indication of the toxicity of the metal to the crabs. In this light, *Uca* is seen to be much more resistant to mercury than the porcelain crab, *Petrolisthes armatus*, in which the 96 h LC_{50} (mean lethal concentration) was 0.050-0.064 ppm (Roesijadi et al. 1974). With long-term exposure to mercury, however, *Uca* can tolerate only 0.18 ppm (Vernberg and O'Hara 1972). In the present study, cadmium might have shown a greater effect than mercury at 0.1 mg/liter because it was absorbed to a much greater extent than the mercury. It is possible that exposure to mercury at levels between 0.1 and 1.0 mg/liter could inhibit regeneration without causing mortality. Despite the high amounts absorbed, lead had no effect on regeneration rate.

At both dose levels of cadmium and the higher concentration of mercury, the retarding effects were greater the first time the experiment was performed (July) than the second (August). Since these crabs normally molt in August, it is probable that they have higher titers of ecdysone at that time, and their progress toward ecdysis cannot be inhibited to the same extent. A similar seasonal difference in sensitivity to cadmium was seen in the shrimp *Paratya tasmaniensis*, which showed a threefold higher LC_{50} value in mid-October than in early July (Thorp and Lake 1974).

Thurberg et al. (1973) have found that cadmium reduced the level of oxygen consumption in the crabs *Carcinus maenas* and *Cancer irroratus*. A reduction of oxygen consumption of the gills of the mud crab, *Eurypanopeus depressus*, exposed to cadmium was found by Collier et al. (1973). Reduced metabolism may be responsible for the retardation of regeneration of the crabs in cadmium. Cadmium has been found to inhibit oxygen consumption and metabolism of fishes (Thurberg and Dawson 1974; Jackim et al. 1970) and has similarly been found to retard fin regeneration in fishes (Weis and Weis in press).

In this sort of study it is difficult to extrapolate laboratory findings to the field. In nature, metals would tend to be concentrated in the sediments more than the water, and it would be primarily from the sediments that these estuarine intertidal crabs would pick up the metals. Crabs would not normally be subjected to the loss of many appendages. Loss of a single limb is not particularly debilitating to a decapod. Should many limbs be lost, however, the crab's locomotion would be impaired, and it would be at a disadvantage. It would therefore be advantageous to regenerate the lost limbs as quickly as possible. Crabs which could not regenerate as quickly could be more subject to predation, and the toxic heavy metal pollutant would then be passed on to higher trophic levels.

Acknowledgments

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NOTES ON THE EARLY DEVELOPMENT OF THE SEA RAVEN, *HEMITRIPTERUS AMERICANUS*

Egg and larval characteristics of the sea raven, *Hemitripterus americanus* (Gmelin), are distinctive. The species ranges from Labrador to Chesapeake Bay but is nowhere abundant (Bigelow and Welsh 1925). Notes on the fertilized eggs (Bean 1897), newly hatched larvae (Warfel and Merriman 1944), and juveniles larger than 45 mm (Huntsman 1922; Bigelow and Welsh 1925; Bigelow and Schroeder 1936) have been recorded. However, there is no available information dealing with specimens between 12 and 45 mm in length. The present paper attempts, in part, to bridge this gap in previous observations of these larvae.

Methods and Materials

A cluster of nearly 90 eggs was found on the rocky shore of Montauk Point, N.Y. The eggs were collected at the level of the high tide mark at 0930 h on 9 November 1974. They were placed in an open system seawater aquarium at the marine station of Southampton College. In mid-December half of the eggs were transferred to laboratory facilities at the Academy of Natural Sciences of Philadelphia, where they were held in artificial seawater (7°C, 32‰) with a controlled photoperiod of 10.5 h light and 13.5 h darkness. Crude but effective temperature control was achieved by placing the covered rearing container in a water bath. The water bath and rearing container were then placed in a refrigerator. The temperature of the water bath was maintained with a thermostatically controlled aquarium heater. A 7½-W light bulb, controlled by an electric timer, was suspended above the rearing container. Moderate aeration kept the eggs in motion. After hatching, the larvae were maintained in similar conditions but without aeration. The strong current resulting from aeration appeared to be detrimental to the fragile larvae. When the yolk was nearly absorbed, the larvae were presented with food in the form of *Artemia* sp. nauplii and small pieces of *Palaemonetes* sp. and *Littorina* sp. flesh. Only three specimens could be induced to eat the pieces of flesh by placing the food in their mouths. Eventually one specimen ate the *Artemia* sp. nauplii unassisted.

Measurements were made on live material. Egg diameters were measured with dial calipers. Total lengths (TL) of the larvae were measured through a dissecting microscope using an ocular micrometer. Myomere counts were made with the aid of two Polaroid[1] HN 38 × 0.3 inch filters placed above and below the larvae and used in conjunction with a dissecting microscope and substage lamp. Final identification of the larvae was based on a comparison of the largest reared specimen in this study and the specimens collected in the Gulf of Maine by Joanne and Wayne Laroche. All 36 preserved specimens were preserved in 5% buffered Formalin and deposited in the Department of Ichthyology, Academy of Natural Sciences of Philadelphia (ANSP 131947).

Descriptions

Egg and Embryo

Some of the peripheral eggs in the cluster had

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

flattened sides, suggesting the cluster had been part of a larger mass. A small piece of an encrusting sponge, *Halichondria panicea*, was found attached to the eggs. Small tubules (0.14 mm in diameter) were also found on the surface of some of the eggs and were assumed to belong to some species of polychaete. Eggs have been described by Warfel and Merriman (1944). At the time of collection, embryos were already well developed in all of the eggs. Pigmentation on the body consisted of melanophores arranged in vertical bars corresponding to the location of the myomeres. The retina was black and the iris had a silvery appearance. The median fin fold and pectoral buds were formed. The former originated close behind the hindbrain. By 16 December, large melanophores developed on the hindbrain and dorsal half of the yolk sac. The body pigmentation ended abruptly on the caudal peduncle about three-fourths of the total length from the snout. This characteristic pattern, to be referred to as the truncated pigmentation pattern, persisted throughout the development of all specimens. The mouth was formed and open. The single oil globule (ca. 0.8 mm in diameter) inside the yolk sac was located at the anterior confluence of the abdomen and yolk sac.

Newly Hatched Larvae

The larvae (Figure 1) began hatching on 3 January 1975, 55 days after collecting the already well developed eggs, and continued through 30 January. The newly hatched larvae averaged 12.8 mm TL (range 11.7-12.7 mm). Warfel and Merriman (1944) noted the larvae emerged head first. This was not always true in the case of my material. Nearly one-half of the larvae which were observed hatching emerged tail first. The large ovoid yolk extended forward to or beyond the posterior margin of the eye. The head was not flexed over the anterior of the yolk sac. Body pigmentation became more dense and uniform but was lacking over the forebrain, ventral half of the yolk sac, and the posterior one-fourth of the body. Melanophores lined the base of the dorsal fin fold to the level of the truncated body pigment. A few melanophores were present along the post-anal fin fold base, near the posterior margin of the body pigment. The preanal fin fold was barely perceptible. No gas bladder developed. The mouth was very large. The maxillary extended to or slightly behind the middle of the eye. The lower jaw contained four sharply pointed, conical teeth on each side. The fourth tooth was somewhat smaller and located lower on the dentary. Body proportions and total myomeres (38 or 39) were similar to those reported by Warfel and Merriman (1944) at this stage. The larvae remained mostly on the bottom of the container, spending much of the time on their sides possibly as a result of the enlarged yolk sac. Efforts to swim were very awkward and only made when the larvae were disturbed.

Further Development

Near the end of January, the larvae were observed to be positively phototactic. The yolk of many of the larvae was absorbed by the end of the first week in February. The peritoneum appeared silvery through the skin. The pigmentation became uniform olive grey over the body (Figure 2). Specimens ranged between 14.0 and 17.0 mm TL on 6 February. Those longer than 16.1 mm had rudimentary caudal rays. The larvae were more

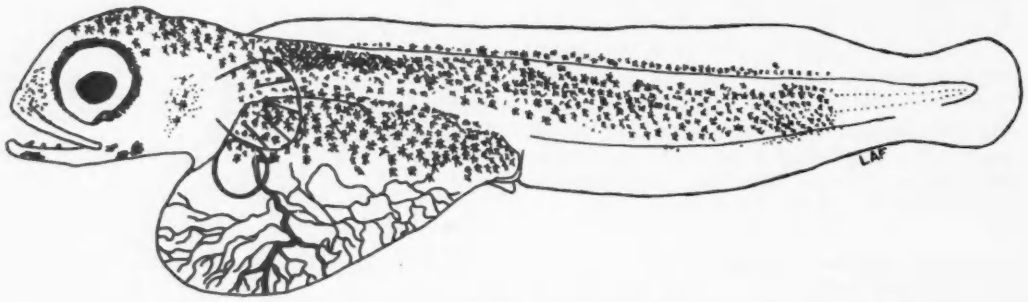

FIGURE 1.—*Hemitripterus americanus*. Prolarva (newly hatched), 8 January 1975: 12.6 mm TL.

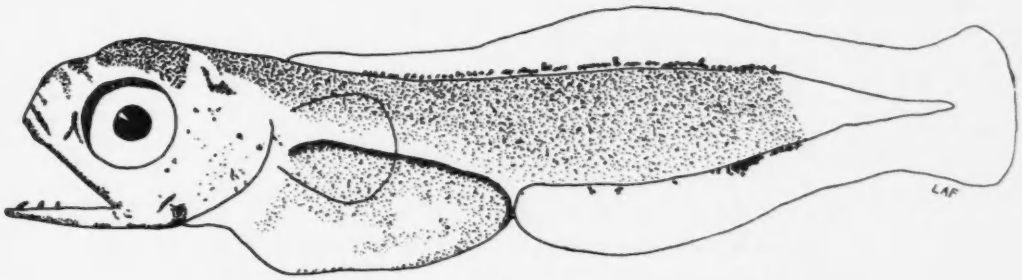

FIGURE 2.—*Hemitripterus americanus*. Early postlarva, 17 February 1975: 15.5 mm TL.

active by this time, but still spent most of the time on the bottom. By 2 March, the larvae were no longer attracted to light.

Toward the end of March, the caudal fin had 8 or 9 ray rudiments. Rays began to develop in the second then first dorsal fins followed by the pectoral fins. The caudal peduncle remained unpigmented. Spines began to form on the preoperculum. Greyish-tan fleshy tabs developed dorsally behind the head and around the occiput.

By 20 April, the largest specimen (Figure 3) had 14 and 11 elements in the first and second dorsal fins, respectively. The anal had 10 rays and the caudal had 12, at about 20 mm TL. Both the dentary and premaxilla had 15 teeth on each side. The preopercular spines became more prominent. The hypural plate began to form. The ratio of the head length to total length was 3.6; of the predorsal length to total length, 3.8; and of the eye diameter to head length, 2.7. The iris became less silvery. Dense pigmentation developed on the interradial membrane of the first dorsal fin between elements 1 through 4 and 8 through 12. Similar pigmentation developed in the second dorsal fin (between elements 3 and 7) and the postanal fin fold (between elements 3 and 6). Few melanophores were scattered between these dense areas of pigment. This larva utilized much of the water column during active periods and spent little time on the bottom.

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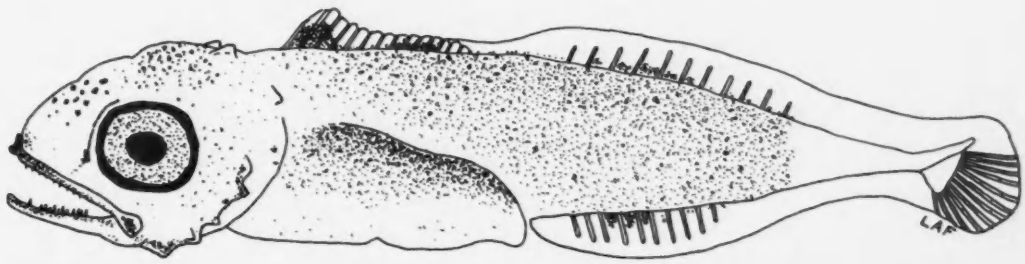

FIGURE 3.—*Hemitripterus americanus*. Postlarva, 20 April 1975: ca. 20 mm TL (the pectoral fin has been deleted for the sake of clarity).

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